

STUDIES ON
THE PHYSIOLOGICAL AND
ECOLOGICAL BACKGROUND
TO THE REPRODUCTION
OF
THE CAPERCAILLIE
(*TETRAO UROGALLUS* LIN.)

BY
VIDAR MARCSTRÖM

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THESIS

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BY

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Fil. lic., Norrl.



Almqvist & Wiksells Boktryckeri AB

UPPSALA 1960

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I. INTRODUCTION

For a long time it has been apparent that the populations of numerous tetraonids have been subject to large numerical fluctuations. Within a few years an abundant occurrence of these birds can be reduced to a small stock. By reason of the prominent place of the tetraonids in the northern fauna their fluctuations have attracted general interest among biologists and hunters as well as among those interested in nature in general. Certain investigators have been of the opinion that good and bad years follow each other in a definite periodic rhythm (cycles). In North America a 10 year periodicity has been claimed for ruffed grouse (*Bonasa umbellus*), while in Europe 3-4 year cycles have been discussed for tetraonids. Other investigators have, however, denied the cyclic regularity of these occurrences, and have regarded the fluctuations as of a more irregular character. In our country no fixed rhythm for the fluctuations in the numbers of tetraonids could be established.

Also with regard to the causes of increases and decreases in the tetraonid stock the opinions of the investigators have been greatly at variance. Attempts have been made in different ways to find a correlation between the numerical fluctuations during a certain period and e.g. ecological or cosmic factors of different kinds. The result has been a succession of theories based on very varying grounds. Because of the very complex nature of the problems, and because of the lack of necessary facts with regard to the influence of certain environmental factors on the species in question, a large part of the extensive literature in this field is of a speculative nature. The person who wishes to make himself more closely acquainted with modern ideas in the research about population dynamics can be referred to among other things a symposium edited by HEWITT (28) and to papers by e.g. SIIVONEN (81) and ERRINGTON (16).

Intensive basic research is, however, required to permit an understanding of the structure and causal relations of the fluctuations in population. Our knowledge of the biology of the different species must be increased step by step, and detailed studies in the field and in controlled environment will have to shed light on the influence of the

food and other environmental factors on the populations. Our present knowledge of the factors that decide the size of the populations, viz. the reproduction up to hatching and the subsequent mortality must be made the basis of future research.

With regard to the tetraonids it can be established that there are no convincing proofs that between different years the number of eggs per clutch or the fertility and hatchability of these eggs display such variations as would substantially affect the size of the stocks. SIIVONEN (81) has certainly found that the average number of eggs per clutch, which with the capercaillie amounts to between 7 and 8, and with the black grouse to between 8 and 9, is somewhat lower for the years which are characterized by a decline in the stocks of birds. He gives, without statistical treatment the difference between years with rising and falling populations to at least 0.2 eggs per clutch. Bearing in mind the great influence of the factors causing losses during the egg stage and the chick stage, no decisive importance for the reproduction result can possibly be attached to this difference.

The loss among eggs up to hatching is fairly substantial, and at the count undertaken in Sweden during the spring of 1953 it could be established that 17% of the 323 capercaillie clutches studied did not hatch for various reasons (33). The reduction in the number of clutches with tetraonids is illustrated also by the Finnish material collected during the years 1946–1952 (81). During these years a total of 1247 nests were studied, and among these the number of destroyed or unhatched clutches varied between 6 and 16%. At the same time it was established that three quarters of this loss was due to direct or indirect influence by human beings, predatory mammals and birds as well as crows, while the causes of the losses of the remaining quarter could not be established with certainty. Thus this quarter included also the eggs that did not hatch as result of low fertility and poor hatchability. It is then interesting to establish that no appreciable difference in the above mentioned ratio ($3/4 + 1/4$) could be observed between different years in spite of the fact that half of these years were years with increasing and the other half years with decreasing stocks. This can be taken as an indication that egg fertility and hatchability were not lower during the unfavourable years, which agrees very well with our observations in Sweden of a high and uniform fertility from year to year among tetraonids.

Also KRISTOFFERSEN (40) and HAGEN (25) arrive at a similar conclusion with regard to the willow grouse in Norway. The former establishes

that the number of eggs which are infertile or whose embryos die before hatching (on average 3.5%) has no significance for the growth of the stock.

Summing up we can establish that variations in different years of reproduction up to hatching do not seem great enough to explain the varying supply of tetraonids.

Consequently attention must first of all be paid to the conditions after hatching and the possibilities for the chicks to reach reproductive age.—Much points in the direction that the loss among tetraonids occurs to an especially large extent among the younger members of the populations, a rule which moreover might apply to most animal species. In certain years especially it has been established that in e.g. capercaillie broods mortality has been very high during the first weeks of life. Nowadays it is also increasingly accepted that in general predators play a relatively subordinated role in this context, and it seems probable that their influence is mainly of secondary importance (cf. p. 57). The whole of this complex problem has, however, been the subject of keen speculation.

As far as the time immediately after the hatching is concerned only the capercaillie has so far been the subject of detailed studies in this respect in our country. HÖGLUND (34), in an interesting study of body temperature, activity, and reproduction in the capercaillie, has been able to establish that the temperature regulation of the chicks during the first weeks of life is imperfect, and that they are thus in need of additional warmth either from the hen or from the environment. The chicks, which in other respects are well developed, begin to look for food already towards the end of the first day. This happens spontaneously without help from the hen which, however, leads the brood and watches over it during their movements on the ground (Fig. 1). Visual impressions dominate the release of the first instinctive pecking movements (35). Development and experience gradually make the search for food so efficient that under favourable weather conditions the chicks can secure their food requirements at an age of 3–4 days (cf. page 57). Under unfavourable weather conditions, on the other hand, the delicate chicks have to spend a longer or shorter time inactive near the hen in order to get from her additional warmth. Less time is thus available for securing the necessary food.¹ Under all conditions the chicks depend,

¹ By way of attempt HÖGLUND (34) made a synopsis covering a number of years of certain data on the climatic conditions near Gävle for the weeks immediately

however, immediately after hatching on food reserves stored in the body. For this reason it has been considered desirable to obtain an insight into the expenditure of these food reserves during the first days after hatching.

A large number of investigations have been made on the embryonic development of birds. The main outlines of the morphological embryology from the single cell stage to hatching is well worked out, and the chemical embryology has made great progress. On the other hand the continued development of the chick immediately after hatching and its connection with the resorption of the yolk, and the transition to procuring its own food has only to a small extent been the subject of investigation.

It is mainly the amount of yolk at hatching and the decrease in its weight in fed and unfed chicks of the domestic fowl which have been studied. This problem has partly an economic background on account of the importance of this question for poultry breeding. On the other hand the chemical metabolism of the yolk has only been the subject of sporadic studies, these processes never having received a clear and in any way complete treatment. The results reported in the literature are often so divergent and also based on such limited experimental material that they have not been carried beyond the stage of hypotheses. After a critical elimination of all more or less uncertain experimental results, the problem of the metabolism of the residual yolk at hatching therefore stands out as being very incompletely investigated.

This question is fundamental from the point of view of game research, since it is of great importance for a thorough knowledge of the reproduction of tetraonids and the problems connected with it. This question has therefore induced the present investigation into the physiology of nutrition of capercaillie chicks during the time immediately after hatching. In the first place the expenditure of the food reserves in fed and unfed individuals—corresponding to situations arising in the field through favourable or unfavourable weather conditions—has been elucidated here, and in this connection attention has been paid to changes in the dry substance of body and liver. Also the influence of the climate on reproduction has been studied in field experiments.

after the hatching of the tetraonids and of the available data on the size of the tetraonid population in the county of Gävleborg. Thereby he observed a certain degree of relation between the maximum temperature in the month of June and the increase of the tetraonid stock.



Fig. 1. Capercaillie hen with her a few day old chicks in search of food. Photo N. Höglund.

With the intention of elucidating the background of the reproduction of the capercaillie conventional methods of chemical analysis have thus been combined with laboratory experiments and field studies. Basic physiologico-ecological investigations of this kind are very sparingly met with in the extensive literature on population dynamics. It is, however, quite clear that populations research of tomorrow will to a much greater extent than hitherto deal with this fundamental borderline field in its efforts to completely elucidate the complex connection between our animal world and its environment.

II. MATERIAL AND METHODS

The capercaillie chicks which were used for these experiments were obtained from eggs laid by wild birds. The eggs distributed over 30 clutches were collected in Hälsingland, Jämtland, Norrbotten, and Lappland. (Some of the chicks in each brood were used for other experiments.) As a rule the capercaillie hen had been sitting on the eggs for a couple of weeks, and the eggs were transported under sitting domestic hens to the experimental station, where they were placed in an incubator. With the capercaillie the incubation time amounts to 26 days. For the sake of comparison it may be mentioned that the incubation time for the domestic fowl is 21 days. Although the eggs were often transported over very long distances, about 90 % of the eggs hatched. Towards the end of the incubation they were transferred to a specially constructed thermostat (46) with the same temperature and humidity as in the incubator.

Immediately after hatching the chicks were extracted through the cuffs on the front of the thermostat, and placed under radiant heaters for the fastest possible drying of the damp embryonic down. After a couple of hours they were dry, and could be weighed (Fig. 2). Then they were marked with a coloured ring round each tarsus; one ring for the number of the clutch and one for the individual. In the text and in the tables the individual chicks have a double number e.g. 45-1 where the first number denotes the number of the clutch, and the second number the number of the individual within this clutch.

The investigations of the expenditure of the food reserves in the capercaillie chick were made by analysing the liver and the part of the yolk sac remaining after hatching for lipids, carbohydrates, and

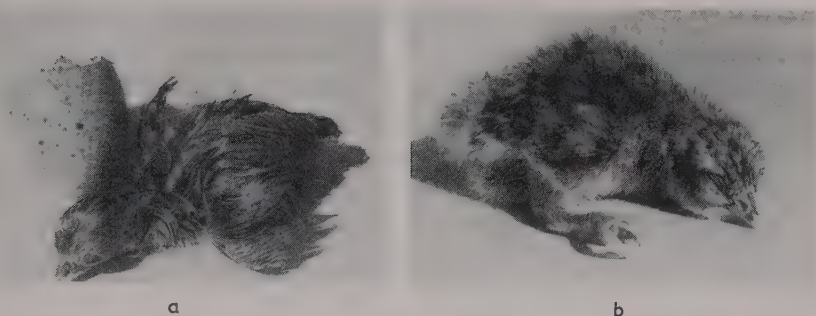


Fig. 2. *a.* Newly hatched capercaillie chick. *b.* The same chick, almost dry. The posture of the chicks is characteristic of this period of rest and sleep which follows the hard work of hatching. Photo N. Höglund.

proteins. Also the amount of body fat¹ was determined, considerable fat deposits associated with the skin being found during the dissections. In connection with these experiments also the percentage of dry substance in the two organs and in the bodies of the chicks was established.

In all 127 capercaillie chicks, distributed into two main groups, fed and unfed, were studied. Since one group was not fed, it was possible to obtain an idea of the importance of the food reserves of newly hatched capercaillie chicks during starvation. Thus these experiments were intended to reproduce the case, when in the field unfavourable weather conditions force the chicks to spend most of the time under the protection of the hen, thus preventing them from feeding. The following age groups were used as suitable: newly hatched, 1, 2.5, 4.5, and 6 day old chicks. During the first day the uptake of food by the capercaillie chicks is quite negligible, although, as mentioned above, they develop a certain pecking activity. Consequently the two youngest age groups were common to the two main groups. During the course of the work it was furthermore found that the starving individuals died before the sixth day. The oldest experimental group among these thereby represents the maximum age which the chicks reached without artificial supply of food. Thus these experimental animals were killed in a very weak condition, when they were slowly passing away.

In text and tables the various groups are designated by three figures followed by a letter. The first figure denotes the age of the chicks in

¹ In this work the word fat, alone or in compounds, refers not only to neutral fat but also to other lipids.

Table 1. Synopsis of the different experimental groups and the number of chicks in each experimental group. (As to symbols and numbering of groups see pages 11–12.)

Experimental group	Number of chicks
0.02 S	21
1.02 S	18
2.13 S	14
4.12 S	16
5.02 S	16
2.13 F	13
4.14 F	15
6.01 F	14

days, the two following figures giving the number of additional hours. The following letter F or S denotes fed and starving chicks, respectively. Thus e.g. 2.13 S denotes that the chicks in question have lived for 2 days and 13 hours, and that they were unfed. For technical and other reasons the age of the individuals in an experimental group can (with the exception of the newly hatched) sometimes vary by some odd hours, and the value given for the different groups is thus a mean value. These variations are, however, so small that they cannot affect the experimental results obtained.

From Table I the distribution of the chicks into the various experimental groups is apparent. However, it has not been possible to avoid miscarriage of some isolated samples. On this account the number of values obtained from an experimental group can be lower than the number of individuals in the group in question.

All experimental animals were kept in rectangular terraria with a heater in one corner, permitting the animals to choose for themselves the most comfortable temperature. All groups had unlimited access to water, and the fed birds given a food that had been used for several years, consisting of bilberry foliage, ant eggs, egg yolk, tender vegetables, "Fors" pheasant food, etc. During the whole time of the experiment they had unlimited access to this food.

The starving individuals behaved on the whole like the fed ones with the single exception that the two oldest groups were somewhat quieter and more inclined to rest than the corresponding groups of fed individuals. Nor did plaintive cries and other signs of discomfort, which

are typical of capercaillie chicks exposed to cold, rain, or other unfavourable influences, occur to any appreciable extent. This could possibly be due to the fact that the chicks had never been fed, and that thus the digestive processes and the peristaltic movements connected with these had not begun to a normal extent, and therefore so marked hunger pains had never developed. For this reason it appears likely that the chicks were not suffering so much due to the condition of starvation to which they were exposed.

The chicks were killed by a stunning blow and by cutting the blood vessels of the throat. By this method post-mortal convulsions were avoided. For upon decapitation the accompanying strong muscular contractions can cause a reduction in the amount of glycogen in the liver (17). Also a slow, though perhaps less marked death struggle has the same effect.

By a rapid dissection the liver and yolk sac were removed and together with the rest of the body immediately frozen to -30°C . They were then stored at this temperature. The liver and the yolk sac were subsequently divided in the frozen condition into three parts for the determination of carbohydrates, lipids, and nitrogen.

In the case of the liver rapid freezing was necessary in order to prevent any post-mortal glycogenolysis that might possibly occur (87). According to WERTHEIMER (93) the liver glycogen in embryos and newly born individuals is on the other hand not so easily mobilised as in fully grown animals, a result which HEYMAN and MODIC (29) have, however, not been able to confirm.

The methods used in this investigation were tried out beforehand by thorough tests on material from domestic fowl which could be obtained more easily. In this way it was possible to establish that, as would be expected, there exist considerable similarities between the physiology of nutrition of domestic chicks and capercaillie chicks. From analyses of different parts of the liver it could furthermore be established that the amount of lipids, carbohydrates, and proteins does not seem to vary to any appreciable extent in different parts of this organ. SWENSSON (87) and a number of other investigators had arrived earlier at a similar result with regard to the distribution of glycogen. SCHEIFF (76), on the other hand, is of the opinion that the concentration of glycogen is not uniform throughout the liver. Owing to the way in which the liver was divided up in my work (cf. below) isolated differences that may possibly occur can hardly have influenced the results.

The difficulties in separating the contents of the yolk sac from the surrounding wall were so great that the entire organ had to be included in the analysis. In domestic chicks, according to RIDDLE (70), semi-solid bodies with a different chemical composition occasionally occur in the contents of the yolk sac which are relatively homogeneous in other respects. In order to eliminate to the greatest possible extent the influence of such irregularities, symmetrical sectors were taken out of the frozen yolk sacs (and livers) for the various analytical determinations. By this procedure a reliable mean value for each experimental group could be counted on.

The lipid analyses were carried out according to Soxhlet by finely dividing the specimens, and then extracting them with a mixture of 1 part alcohol and 10 parts ether. For liver and yolk a mixture of 1 part alcohol and 15 parts ether was used (cf. 97). The large addition of ether was used mainly in order to get the free lipids included, and to reduce to the greatest possible extent the amount of lipo-protein complexes. It is, however, not possible completely to dispense with alcohol, since pure ether does not mix with specimens containing water. For the purpose of control the specimens were in some cases divided into two parts, of which one part was analysed according to the method mentioned above, while the other part was freeze-dried, and extracted solely with ether. The analytical results obtained by these two methods did not differ significantly from each other.

The total amount of carbohydrates was determined according to a method described by SØRENSEN and HAUGAARD (90) and modified by LØVTRUP (51). In this method orcinol was used. As a rule the commercial product was so impure that it had to be re-crystallized. The extinction of the samples was read off in a Beckman spectro-photometer at 420 $m\mu$. In order to obtain as accurate results as possible duplicate determinations were always performed. It can be pointed out that these analyses which were carried out on yolk sac or liver did not vary more than those which were carried out on a glucose solution. The error with the orcinol method was in no experimental group found to be more than 3.3 per cent.¹

The nitrogen analyses were carried out according to PARNAS-WAGNER

¹ The formula used was $\sigma m = \sqrt{\frac{\sum d^2}{2n}}$ (after Dahlberg, G., 1940: Statistical Methods

for Medical and Biological Students, London), where d is the difference between the two values obtained for the same sample, n the number of differences, and σm the error.

(62). The amount of Kjeldahl nitrogen in mg multiplied by 6.25 is regarded as the total amount of proteins in this work. Two analyses were performed on each sample and the difference between the values obtained never exceeded 2%.

The amount of dry substance was determined by weighing the extraction thimbles used for the lipid analyses after the lipids had been extracted, and the thimbles had been dried to a constant weight at a temperature of +80°C. The weight of the empty thimbles was deducted, and the weight of lipids extracted was added to the values obtained.

For the investigation of the functional significance of the yolk stalk (page 22), a method for determining chromium oxide according to EDIN, KIHLEN and NORDFELDT (13) was used.¹

Finally the amount of cholesterol in the bodies of the chicks was determined by Liebermann-Burchard's colour reaction² (74).

III. AN ATTEMPT TO CONTROL SYSTEMATIC ERRORS OF THE ANALYTICAL METHODS

An idea of the reliability of the methods employed in this work can be obtained by the following simple arithmetical process: the amounts of carbohydrates, proteins, lipids, and water in liver and yolk sac, expressed as a percentage of the wet weight of the organs, are added up for each experimental group (Tables 2 and 3).

The sum values for the liver of the various experimental groups lie close to 100 or on an average slightly below. This must be regarded as a remarkably good agreement with the theoretical value which ought to lie a couple of units below 100, since a mineral content of nearly 2% of the wet weight can be counted with in this organ (85).

Also the sum values for the yolk lie very close to the theoretical value with the exception of the value for group 4.14 F which deviates more substantially with a value of 92.31%. This deviation can, however, not be regarded as particularly remarkable bearing in mind the small amounts of yolk, the surrounding epithelium of which could possibly

¹ All chromium analyses were carried out at Statens husdjursförsök, Kgl. Lantbrukshögskolan, Ultuna.

² The analyses were carried out at Stockholms läns Centrallasarett.

Table 2. The relative amount of the most important chemical constituents of the wet weight of the liver in the fed and unfed capercaillie chicks.

Experimental group	Percentage composition				
	Carbo-hydrates	Proteins	Lipids	Water	Total
0.02 S	1.28	14.69	17.60	66.76	100.33
1.02 S	1.42	16.49	16.99	66.00	100.90
2.13 S	1.33	17.57	17.57	63.66	100.13
4.12 S	1.04	17.04	19.47	62.13	99.68
5.02 S	0.95	16.50	18.80	62.81	99.06
0.02 (F)	Same as group 0.02 S				
1.02 (F)	" " " 1.02 S				
2.13 F	2.58	15.82	16.96	64.80	100.16
4.14 F	3.32	15.51	11.82	68.13	98.78
6.01 F	5.14	14.74	9.23	69.82	98.93

Table 3. The relative amount of the most important chemical constituents of the wet weight of the yolk sac in the fed and unfed capercaillie chicks.

Experimental group	Percentage composition				
	Carbo-hydrates	Proteins	Lipids	Water	Total
0.02 S	1.45	22.80	29.12	43.61	96.98
1.02 S	1.35	22.35	27.58	44.85	96.13
2.13 S	1.32	17.59	28.52	49.05	96.48
4.12 S	0.63	9.40	20.50	67.69	98.22
5.02 S	0.57	9.25	17.86	71.23	98.91
0.02 (F)	Same as group 0.02 S				
1.02 (F)	" " " 1.02 S				
2.13 F	1.24	18.05	27.50	49.74	96.53
4.14 F	0.76	7.63	27.47	56.45	92.31
6.01 F	No analyses carried out				

upset the analyses. The mineral content of the yolk is of the same magnitude as that of the liver.

Against the background of the above facts we might be entitled to assert that the analytical methods employed have a high degree of reliability.

IV. RESULTS AND GENERAL DISCUSSION

A. The Total and Reduced Body Weight as Wet Weight and Dry Weight

Each brood of chicks was distributed over several experimental groups. The average weight at hatching varies between 37.24 and 37.91 g for 7 of the 8 experimental groups (cf. Table 4), although the weight of the chicks can vary considerably between the different broods and even within the same brood. Group 6.01 F has on the other hand an average weight of 39.46 g at hatching, and thus differs significantly

Table 4. Data on the wet weight and dry weight of the body in the fed and unfed capercaillie chicks.

Experimental group	Body weight (g)				Reduced dry weight of the body (yolk sac and liver not included) (g)	n	Per cent dry substance in the body (yolk sac and liver not included)	n
	At hatching	At the end of the experiment	Difference	n				
0.02 S	37.91 ± 0.65	37.91 ± 0.65		21	6.42 ± 0.14	21	20.97 ± 0.14	20
1.02 S	37.54 ± 0.80	35.10 ± 0.73	- 2.44 ± 0.24	18	7.19 ± 0.12	16	23.10 ± 0.20	16
2.13 S	37.88 ± 0.83	33.20 ± 0.81	- 4.68 ± 0.25	14	7.10 ± 0.14	12	23.02 ± 0.23	12
4.12 S	37.24 ± 0.69	28.68 ± 0.61	- 8.56 ± 0.43	16	6.27 ± 0.10	15	22.75 ± 0.27	13
5.02 S	37.70 ± 0.42	28.18 ± 0.51	- 9.52	16	6.09 ± 0.13	14	22.69 ± 0.12	15
			- 9.82 ± 0.24 ^a	13				
2.13 F	37.31 ± 0.40	36.15 ± 0.45	- 1.18 ± 0.30	13	8.03 ± 0.19	12	23.84 ± 0.29	12
4.14 F	37.77 ± 0.65	41.60 ± 1.16	+ 3.84	15	9.22 ± 0.33	13	23.49 ± 0.26	13
			+ 4.16 ± 0.75 ^a	14				
6.01 F	39.46 ± 0.62	48.18 ± 1.24	+ 8.75 ± 1.33	14	10.88 ± 0.31	13	23.49 ± 0.23	13

^a Cf. page 27.

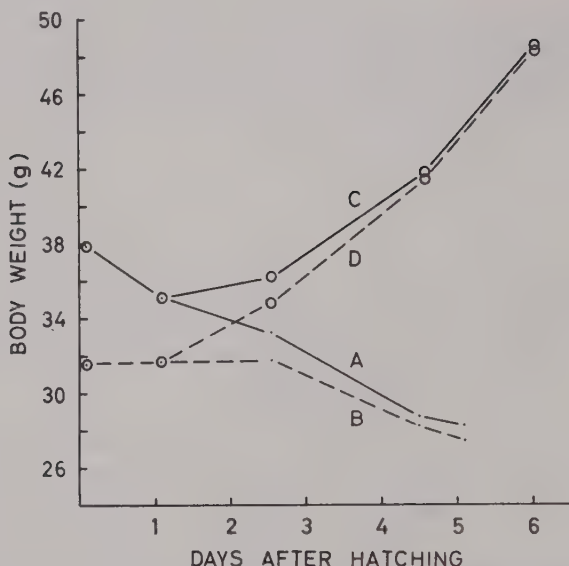


Fig. 3. The total (—) and the reduced body weight (yolk sac not included) (-----) in the groups of fed (○) and unfed (·) capercaillie chicks.

from the others ($t=2.73$, $f=125$, $p<0.005$). However, this difference has not influenced the results of the completed investigations to any considerable extent. From the point of view of comparison this group is also of subordinate importance, since its chicks are about 1 day older than the oldest of the unfed chicks. It should moreover be pointed out that as a rule the analytical results for the fed chicks vary considerably more than for the corresponding groups of unfed chicks. This is due to the more uniform nutritional conditions within the unfed groups.

Fig. 3 shows the total body weight (wet weight) of the unfed chicks to decrease relatively uniformly during the whole of the experimental period (curve A). If, on the other hand, the weight of the yolk sac is deducted from the total body weight, curve B then shows the accordingly reduced body weight in unfed chicks to be constant during the first 2.5 days. The horizontal course of curve B should indicate that the food substances which are resorbed from the yolk sac during the first 2.5 days are used solely for the maintenance of the chicks' catabolism. In an experiment with a small number of unfed domestic chicks ILJIN (37) observes that the dry weight of the body (the yolk being deducted) is comparatively constant during the first days after hatching. However,

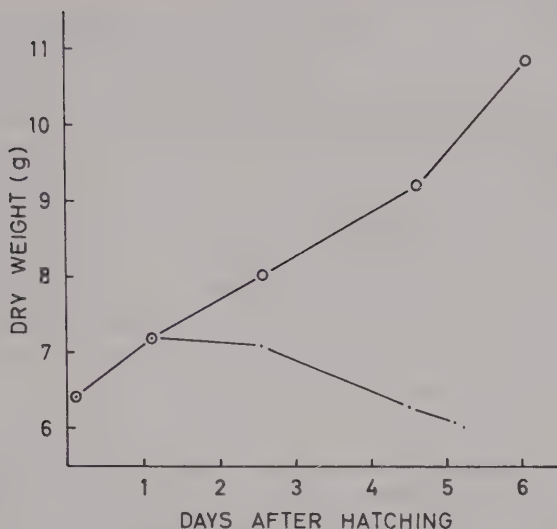


Fig. 4. The reduced dry weight of the body (yolk sac and liver not included) in the groups of fed (○) and unfed (·) capercaillie chicks.

from Table 4 and Fig. 4 it can be seen that the dry weight of the capercaillie chicks (the yolk sac and the liver being deducted) increases considerably, viz. from 6.42 g at hatching to 7.19 g ($t=4.09$, $f=35$, $p < 0.0005$) a day later, and also the dry weight of the liver increases considerably during this period (cf. page 38). This substantial increase in the dry weight during the first day of life thus implies, contrary to what was suggested above, that part of the food substances which are liberated from the yolk during this period are not used up immediately, but are stored in the body (cf. page 32). However, the above apparently conflicting experimental results are explained if they are compared to Fig. 5 which shows the amount of dry matter as a percentage of the chicks' body weight (the yolk and liver being deducted). Thus it is evident that during the chicks' first day of life a decrease in the water content of the tissues takes place so that the percentage of dry substance is increased from 20.97 to 23.10% ($t=8.75$, $f=34$, $p < 0.0005$). It afterwards remains constant in unfed chicks. Thus owing to the marked decrease of the water content in the tissues of the chicks' body during the first day of life the relatively substantial increase of the dry weight during this period is not reflected in a corresponding increase in the chicks' wet weight.

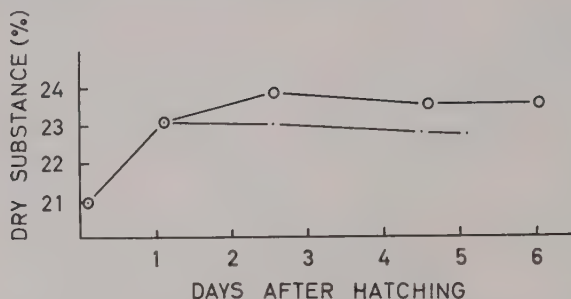


Fig. 5. Percentage of dry substance in the body (yolk sac and liver not included) in the groups of fed (○) and unfed (·) capercaillie chicks.

In order to see these facts in a larger context, it is necessary to go back to the conditions before hatching. In a small number of already mentioned experiments with domestic chick embryos ILJIN has observed that the percentage of water in the body decreases during the incubation. A closer examination of his results indicates that this continuing decrease in the water content of the body tissues of the embryo nevertheless stops 2–3 days before hatching. POHLMAN (67) has been able to show by dry weight determinations on certain parts of the muscles that the invagination of the yolk into the abdominal cavity a couple of days before hatching is accompanied by a substantial increase of the water content of the embryo of the domestic chick. This increase is more or less pronounced in different parts of the body. This fluid infiltration reaches its maximum at hatching, and afterwards decreases again. A table given by ROMANOFF (71) also shows that the percentage of dry substance in the embryo is highest three days before hatching. It is difficult to express an opinion on the causes of the demonstrated increase of fluid on the basis of experiments made up to now. NEEDHAM (57) considers the absorption of fluids into allantois and amnion, and a certain inability of the kidneys to take care of the water surplus in the body to be likely causes.

In conclusion it can nevertheless be established that the decrease in the water content of the tissues of the embryo, that ceased at the invagination of the yolk, is continued again after hatching. Lung respiration and a growing excretion from the kidneys increases the loss of water while at the same time during the first day of life the chicks' consumption of water is quite negligible. However, a certain

amount of fluid is supplied to the body by the resorption of the yolk sac which according to Table 6 decreases during the first day of life by roughly 3 g of which amount 1.3 g are water.

From Figs. 3, 4, and 5 it is evident that wet weight, dry weight, and the percentage of dry substance are on the whole constant in *unfed* birds from 1 to 2.5 days after hatching. This indicates that during this time no storing of food substances takes place in the body. Afterwards, during the remaining time of the experiments, both wet weight and dry weight decrease rather markedly owing to a desaggregation of the food substances stored in the body tissues (cf. page 52).

In the *fed* capercaillie chicks the weight ratios discussed here are in part different. However, this is not the case during the first day of life during which the chicks do not consume any food, and fed and unfed chicks can therefore be grouped together. As has already been mentioned the resorption of the yolk causes a rapid decrease of the total body weight during this period (cf. Fig. 3). Afterwards, however, it begins to increase, so that at an age of a good 3 days the fed capercaillie chicks weigh as much as they did at hatching. The reduced body weight (with the yolk deducted) is constant during the first day of life, but then also this increases continuously. The relative increase in weight seems to augment with growing age in the young chicks (cf. 34), although part of the increase between 4.5 and 6 days may possibly be referable to the higher weight at hatching of the oldest experimental group. The dry weight of the fed chicks (the yolk being deducted) increases on the whole continuously during the whole time of the experiments, although also here a more substantial rise is noticed between the ages of 4.5 and 6 days (Fig. 4). The percentage of dry substance in the body is somewhat higher in fed than in unfed chicks. This is probably connected with the larger amount of body fat in the former. At an age of 2.5 days the fed ones have 23.84% dry substance, and the unfed ones 23.02% (the difference = 0.82, $t = 2.23$, $f = 22$, $p < 0.025$). At the age of 4.5 days on the other hand the difference is not statistically significant.

B. The Yolk Sac

1. *The Anatomy of the Yolk Sac and the Function of the Yolk Duct.*

The yolk sac is filled with the non-resorbed remainder of the egg yolk, and is invaginated into the abdominal cavity towards the end

of incubation. On the inner side its thin wall has folds or inwardly directed septa, and the whole surface is covered with a special glandular epithelium with an absorbing function (26). The yolk sac is furthermore supplied with a rich network of blood vessels which, like the inwardly directed folds ramify most richly round its equator (Fig. 6). By the cavity of the yolk stalk (the yolk duct), the yolk sac is connected with the small intestine. According to HAMILTON no yolk is however transported through this duct, but all resorption takes place by means of the richly ramifying net of blood vessels. ILJIN, however, is of a completely opposite opinion, and considers that the yolk is extracted through the yolk duct with the help of the abdominal muscles, and he describes further how an intestinal fold covers the opening of the yolk duct, preventing food particles from being forced from the intestine into the yolk sac.

In order to decide, whether or not a transport of material actually occurs through the yolk duct, the author injected chromium oxide (Cr_2O_3), suspended in a physiological salt solution, through the wall of the abdomen into the yolk sac of 10 newly hatched domestic chicks.¹ These chicks did not receive any food during the following days. Their faeces and, after they had been killed some days later, their intestinal contents were examined for the presence of chromium. Both the intestine and the faeces were found to contain chromium oxide. By reason of its particle size this cannot pass into the blood, but must have been transported into the intestine via the yolk duct. Unfortunately it is not possible to obtain a uniform distribution of the injected test substance in the whole of the yolk sac, and it is thus impossible to establish how great a part of the contents of the yolk sac passes through the yolk duct. There is on the other hand no doubt that part of the yolk is also resorbed via the numerous blood vessels of the yolk sac.

2. *Wet Weight and Dry Substance.*

The quantity of yolk in the newly hatched capercaillie chick is considerable. Its weight varies in group 0.02 S between 4.38 and 9.84 g. As shown in Table 5 and Fig. 7 the weight of the yolk is positively correlated with the chicks' total body weight at hatching ($r=0.631$, $v^2=12.54$, $p<0.005$). There exists on the other hand no such connection, if the weight of the yolk sac is put into relation to the reduced

¹ For this suggestion I wish to thank Prof. P. E. Lindahl.



Fig. 6. Liver (1), yolk sac (2), and alimentary canal with gizzard (3) from a newly hatched capercaillie chick. Note the narrow yolk duct (4) and the richly ramifying blood vessels round the equator of the yolk sac. Photo N. Hoglund-V. Marcström.

Table 5. The wet weight of the body and yolk sac, and the percentage relation between these weights in newly hatched capercaillie chicks (0.02 S).

Number of chick	Body weight (g)	Yolk sac	
		Wet weight (g)	Percentage of body weight
15-3	38.26	4.91	12.83
16-5	39.06	5.45	13.95
22-2	38.53	6.75	17.52
25-5	39.88	5.86	14.69
45-3	33.28	4.76	14.30
46-4	35.32	6.40	18.12
49-2	35.54	5.84	16.43
-3	33.70	4.38	13.00
-4	31.10	4.61	14.82
52-3	38.25	8.46	22.12
-6	35.25	7.66	21.73
53-1	37.49	5.90	15.74
55-2	40.67	6.23	15.32
-4	39.10	5.72	14.63
59-5	38.80	6.09	15.70
60-2	43.07	9.84	22.85
-4	42.05	8.23	19.57
-7	40.92	7.05	17.23
63-5	37.59	5.58	14.84
64-5	38.43	5.84	15.20
-6	39.81	6.78	17.03

body weight (without yolk sac) of the chicks. This applies to wet weights as well as dry weights. This implies that individuals with great weight of body (without yolk sac) have no particularly big yolk. However, the size of the yolk sac can sometimes vary considerably even in individuals of the same size. As a percentage of the total body weight the weight of the yolk can fluctuate between 12.83 and 22.83 % with 16.55 % as the mean value. In comparison it can be mentioned that according to my own investigations the yolk of domestic chicks amounts to $22.01 \pm 0.53\%$ ($n=10$) of the body weight.

A remarkable agreement exists on the other hand concerning the amount of yolk as a percentage of the body weight in capercaillie chicks from the same brood. The distribution of the broods into

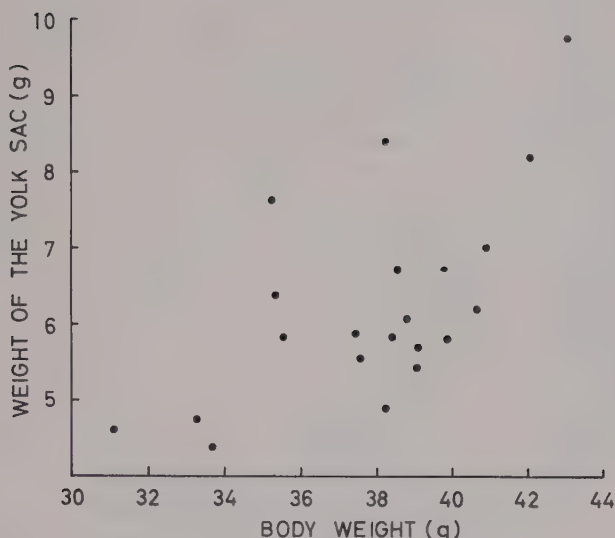


Fig. 7. The relation between the weight of the yolk sac and the total body weight in newly hatched capercaillie chicks.

different experimental groups permits, however, the comparison of only a small number of chicks at this stage (Table 5). The amount of yolk in broods 49 and 55 lies for all the chicks below the mean value of 16.55%, while on the other hand the amount of yolk in broods 52 and 60 considerably exceeds this value. Brood 64 on the other hand seems to lie around the mean value. This agreement within the broods, as well as the differences in this respect between the broods, must have a genetic basis. These observations confirm earlier investigations on domestic chicks carried out by JULI and HEYWANG (38). These investigators found that the percentage of yolk in unincubated egg varies significantly between different hens, and that the genetic constitution of the hen also determines the rate at which the assimilation of the yolk continues during embryonic development.

The resorption of the yolk takes place at a somewhat slower rate in the starving chicks than in the fed ones, and thus the rate of resorption is sped up by feeding (Fig. 8 and Table 6). Consequently the fact that the chicks begin to eat during the second day of their life produces a difference in the size of the yolk sac. At the age of 4.5 days it weighs 0.32 g in the fed chicks,¹ while in the unfed ones it amounts

¹ One chick is not included in this value (cf. page 27).

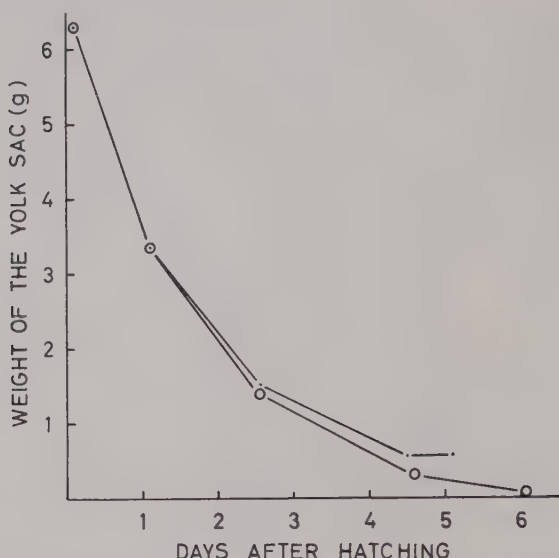


Fig. 8. The wet weight of the yolk sac in the groups of fed (O) and unfed (·) capercaillie chicks.

to 0.55 g ($t=5.68$, $f=26$, $p<0.0005$). Different age does not allow comparison of the two oldest experimental groups, although the tendency seems to be quite clear also in this case. The above result is in contrast to the statement which NEEDHAM (57) makes about the yolk sac on the basis of ILJIN's investigations in this field: "No doubt it takes a long time to disappear completely if the circumstances of post-natal life are favourable to survival." Other authors, among them SCHILLING and BLEEKER (77), PARKER (61) and HEYWANG and JULL (30) are of a different opinion as they have not been able to observe any difference between the resorption of yolk in fed and unfed chicks. These divergent results are probably due to several reasons. In some cases the experimental animals seem to have been so few that no significant difference has appeared. In other cases the experiments have not been extended over a sufficiently long time. From Fig. 8 it is evident that the resorption of the yolk is a process the rate of which decreases with growing age. Thus during the first day 3 g of the 6.3 g weight of the yolk sac, or roughly 47%, is consumed. This makes obvious the importance of exactly determining the time of hatching of the chicks, if a reliable knowledge of the metabolic processes connected with the

Table 6. Wet weight, dry weight, and percentage of dry substance in the yolk sac of the fed and unfed capercaillie chicks.

Experimental group	Wet weight (g)	<i>n</i>	Dry weight (g)	Dry substance (%)	<i>n</i>
0.02 S	6.30 ± 0.30	21	3.618 ± 0.182	56.39 ± 0.53	19
1.02 S	3.34 ± 0.25	18	1.837 ± 0.135	55.15 ± 0.64	15
2.13 S	1.50 ± 0.21	14	0.795 ± 0.134	50.95 ± 1.66	12
4.12 S	0.55 ± 0.03	14	0.183 ± 0.015	32.31 ± 1.43	13
5.02 S	0.74	16	0.233	28.77	14
	0.56 ± 0.06 ^a	13	0.152 ± 0.014 ^a	27.20 ± 1.10 ^a	11
2.13 F	1.39 ± 0.19	13	0.714 ± 0.112	50.26 ± 0.69	12
4.14 F	0.42	15	0.184	43.55	13
	0.32 ± 0.03 ^a	14	0.142 ± 0.016 ^a	44.06 ± 1.17 ^a	12
6.01 F	0.08 ± 0.01	14			

^a Cf. below.

resorption of the yolk immediately after hatching is desired. In earlier investigations the age of the chicks has sometimes been counted from the time, when they were taken from the incubators (cf. e.g. page 38). With a large hatch this can mean that several individuals are then considerably more than one day old. The outcome in such cases must be conflicting experimental results.

Otherwise the resorption of the yolk seems to take place in such a way that capercaillie chicks which at hatching dispose over a large amount of yolk also consume more of it per time unit. This process diminishes, with increasing age, the considerable difference (5.46 g) existing at hatching between the largest and the smallest yolk sac.

Together with the continuous yolk resorption in most of the chicks individual deviations occur nevertheless in certain cases. In Table 6 and 7 two values are entered in each column for the groups 5.02 S and 4.14 F (cf. also Table 4). Of these the upper figure gives the mean value for all chicks, while the lower figure does not include the chicks with yolk sacs which differ markedly in size from the otherwise relatively equally sized majority. This latter value should thus be regarded as being more representative of the group in question, and has therefore been used in the Figures (8–10) which illustrate the yolk sac.

Group 4.14 F includes one chick which with a yolk weight of 1.82 g

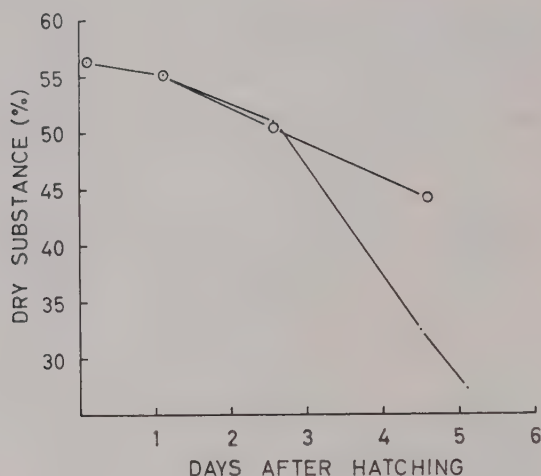


Fig. 9. Percentage of dry substance in the yolk sac in the groups of fed (○) and unfed (●) capercaillie chicks.

differs considerably from the mean value of 0.32 g of the rest. This disturbance of the yolk metabolism is reflected also in a reduction of the body weight by 0.84 g, while in the other chicks in this group it has augmented by 4.16 g on the average. At the same time the water concentration of the yolk in question is 17–18% higher than in the rest of the yolks of the same size. In the oldest unfed experimental group, viz. 5.02 S, 3 chicks have yolk sacs that differ to an exceptional degree from the mean weight for the rest of the group. Their yolks weigh 1.32, 1.47, and 1.82 g, while the mean value for the rest of the chicks in this group is 0.56 g. The water concentration of these three yolk sacs is at about the same level as in that of the chick referred to earlier.

During the incubation period the water concentration of the yolk fluctuates considerably (70, 71, 57). According to ROMANOFF the percentage of dry substance in the yolk of the domestic hen's egg decreases by full 10 units during the first week of incubation, in order to increase subsequently by more than 20 units up to the 17th day, when it reaches its maximum value. After this it decreases again towards the end of the incubation, probably on account of the rapid expenditure of lipids during this period. One day before hatching (the 20th day of incubation) the percentage of dry substance in the yolk sac is thus 4–5 units higher than at the beginning of the incubation, or according to ROMANOFF

57.12 %. In the newly hatched capercaillie chick the corresponding value is 56.39 %.

The decrease in the percentage of dry substance in the yolk sac which takes place during the latter part of the incubation, is continued also after hatching, and is greatest in the unfed chicks after the age of 2.5 days (Table 6 and Fig. 9). Thus the percentage of dry substance of the yolk sac decreases in the fed chicks from 50.26 % at the age of 2.5 days to 44.06 % at the age of 4.5 days (difference = 6.20 %, $t = 4.57$, $f = 22$, $p < 0.0005$). On account of the very small size of the yolks no determinations have been made in the oldest age group of the fed chicks. In the unfed chicks the decrease from 2.5 to 4.5 days is more than twice as high, or from 50.95 % to 32.31 %, and continues also up to the age of 5 days. From this it follows that the difference in the yolk resorption between fed and unfed chicks, which has been established earlier on the basis of the wet weight of the yolk sac at the age of 4.5 days, is not clearly noticeable if the dry weight is taken as a starting point (difference = 0.041 g, $t = 1.91$, $f = 23$, $p < 0.05$).

Table 7. The amount of carbohydrates, proteins, and lipids in the yolk sac of the fed and unfed capercaillie chicks.

Experimental group	Carbohydrates			Proteins			Lipids		
	mg	% of the wet weight of the yolk sac	n	mg	% of the wet weight of the yolk sac	n	mg	% of the wet weight of the yolk sac	n
0.02 S	91.3 ± 4.9	1.45 ± 0.03	19	1471 ± 94	22.80 ± 0.55	20	1832 ± 89	29.12 ± 0.67	20
1.02 S	46.7 ± 4.1	1.35 ± 0.06	16	784 ± 70	22.35 ± 0.50	16	916 ± 68	27.58 ± 0.98	15
2.13 S	20.8 ± 3.8	1.32 ± 0.06	12	283 ± 55	17.59 ± 1.01	12	434 ± 60	28.52 ± 0.98	14
4.12 S	3.6 ± 0.4	0.63 ± 0.06	13	54 ± 4	9.40 ± 0.47	13	115 ± 7	20.50 ± 0.94	13
5.02 S	4.5	0.57	14	81	9.25	14	148	17.86	15
	3.1 ± 0.3 ^a	0.55 ± 0.04 ^a	11	45 ± 6 ^a	8.02 ± 0.75 ^a	11	102 ± 11 ^a	17.03 ± 0.66 ^a	12
2.13 F	19.1 ± 4.4	1.24 ± 0.10	11	284 ± 69	18.05 ± 1.61	11	367 ± 44	27.50 ± 1.25	12
4.14 F	3.5	0.76	12	44	7.63	13	110	27.47	13
	2.4 ± 0.3 ^a	0.75 ± 0.05 ^a	11	23 ± 3 ^a	6.92 ± 0.27 ^a	12	93 ± 12 ^a	28.31 ± 1.61 ^a	12
6.01 F	—	—		—	—		—	—	

^a Cf. page 27.

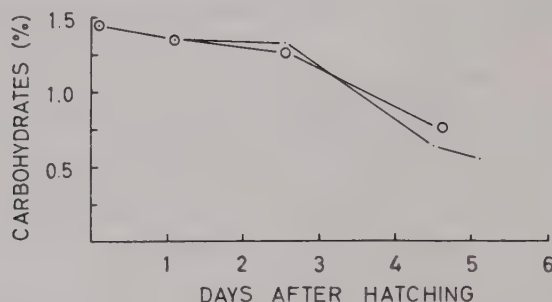


Fig. 10. Percentage of carbohydrates in the wet weight of the yolk sac in the groups of fed (○) and unfed (●) capercaillie chicks.

3. Carbohydrates.

According to ROMANOFF and ROMANOFF (72) the yolk of the domestic hen's egg contains only about 1% carbohydrates. According to numerous determinations the main part of these seems to occur in the free form, and a smaller part in combination with proteins and lipids. SAKURAGI (75, quoted from 57), IIZUMI (36), and others have proved that small amounts occur in the form of glycogen. During incubation the amount of carbohydrates in the yolk decreases, and according to NEEDHAM (57) about 50 mg of free sugar constitutes at hatching the main part of the remaining carbohydrate reserve in the yolk sac of the domestic chick. It is impossible to form an idea of the size of the yolk sac in this case.

The yolk sac of the newly hatched capercaillie chick contains on the average 91.3 mg carbohydrates (Table 7), or 1.45% of the wet weight of the yolk sac. Up to 2.5 days after hatching the carbohydrates of the yolk are used up at about the same rate as its weight decreases. However, after the age of 2.5 days a rapid decrease of the carbohydrate concentration of the yolk sac takes place in fed as well as unfed chicks (Fig. 10). With regard to the carbohydrate expenditure in the yolk sac no fundamental difference seems to exist between the fed and unfed chicks.

4. Proteins.

During the embryonic development of the egg of the domestic hen the protein concentration in the yolk increases because of the dominating fat catabolism. MURRAY (54) and FISKE and BOYDEN (20) like earlier investigators found that fat is the main source of energy for

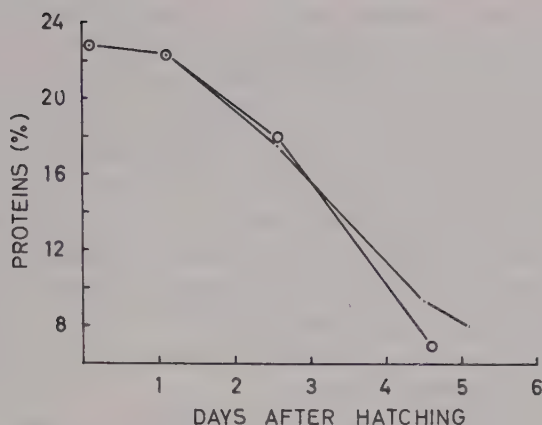


Fig. 11. Percentage of proteins in the wet weight of the yolk sac in the groups of fed (○) and unfed (·) capercaillie chicks.

the growing embryo. According to NEEDHAM (57) 91% of the food substances which are catabolized in the egg during incubation consist of fat, 5–6% of proteins and 3–4% of carbohydrates. The yolk in the egg of the domestic hen at the beginning of incubation contains 16.5% proteins while the corresponding value at the end of incubation according to a small number (8) of analyses of my own varies between 23.5 and 29%. The amount of proteins in the newly hatched capercaillie chick's yolk sac amounts on an average to 1.471 g or to 22.80% (Table 7). After one day almost half of this has already been consumed, and after this protein resorption takes place more rapidly than the decrease of weight of the yolk. This causes a rapid decrease of the protein concentration (Fig. 11). There is no difference in this respect between fed and unfed chicks.

During the embryonic development the proteins of the egg are used mainly for the building up of the growing embryo, and only a small part is used for catabolism (cf. above). On the basis of the very summary studies by ILJIN (37) already mentioned earlier, of the dry weight of starving domestic chicks, NEEDHAM (57) states that all that is required for the building up of the embryo has been resorbed before hatching, and that the remaining part of the yolk is then completely catabolized. He further concludes against the background of this statement that fat catabolism, which is dominant towards the end of incuba-

tion (56, 58), gives place after hatching to a catabolism in which the proteins play a prominent part as substrate.

It might, however, be of interest, on the basis of the results presented, to subject his scarcely wellfounded opinion to a critical examination. It then appears as if the demonstrated increase of the protein concentration of the yolk sac during incubation (cf. page 31) should imply conditions for an increased protein metabolism after hatching, but it says nothing about the intensity of the protein catabolism. However, on the basis of changes in the dry weight and fat depots of the *unfed* chicks, and of the amount of proteins absorbed from the yolk during the same time, it is possible to obtain a relatively good idea of the magnitude of the protein catabolism.

From Table 8 it appears that the dry weight of the chick (yolk sac and liver not included) during the first day of life increases by 0.770 g ($t=4.09$, $f=35$, $p<0.0005$) of which 0.101 g consists of lipids. This increase of the lipids is not statistically significant, and it must thus be assumed that the additional dry substance is derived mainly from proteins. At the same time the amount of proteins in the liver increases during the first day by 0.052 g ($t=11.49$, $f=31$, $p<0.0005$). Consequently that part of the dry substance of the capercaillie chick which ought primarily to be derived from the proteins of the yolk sac, has increased in all by 0.822 g ($0.770+0.052$) during the period in question. On the other hand not more than 0.687 g of protein has disappeared from the yolk sac implying that about 0.135 g ($0.822-0.687$) of the additional dry substance which has appeared during the first day of life is not derived from proteins. A building up in the body of glycogen, which has been used during the difficult hatching phase is, however, possible (cf. page 42). Further it is necessary to take into account that a few tens of milligrams of inorganic material has also been stored in connection with the rapid metabolism of the yolk material and the large increase in the dry weight of the body. Finally it is hardly excluded that a small amount of lipids has been supplied to the body from the yolk sac, although the increase in the amount of lipids in the body is not statistically established, as has been pointed out above.

On the basis of these experimental results the following important conclusion can be drawn:

1) At hatching the yolk sac still contains considerable amounts of material for synthetic purposes.

Table 8. Comparison of the dry weight and amount of lipids in the body, and the amount of proteins in the yolk sac and liver in unfed capercaillie chicks during their first day of life.

Compared components	At hatching (g)	At age of 1 day (g)	Difference (g)
Dry weight of body (yolk sac and liver not included)	6.420	7.190	+ 0.770
Body lipids (yolk sac and liver not included)	1.798	1.899	+ 0.101
Liver proteins	0.107	0.159	+ 0.052
Yolk sac proteins	1.471	0.784	- 0.687

2) During the first day of life the chick's fat catabolism predominates entirely, just as before hatching. As much as 0.940 g is resorbed from the yolk sac. An insignificant amount of carbohydrates is utilized, and proteins do not appear to be used as a source of energy to any appreciable extent.

Thus it is clear that NEEDHAM's opinion about the increase of protein catabolism immediately after hatching must be modified. Other investigators also have taken up for more detailed consideration the question of the protein metabolism in the newly hatched chicks. The results have, however, been so divergent that they have as a rule been regarded with much scepticism. On the basis of the amount of uric acid excreted, according to FRIDERICIA (22), by domestic chicks during the two to three first days of life, NEEDHAM (57) estimates the protein catabolism to 266 mg per 100 g body weight per day or about 100 mg per day per chick. However, ROMENSKY's (73, quoted from 57) investigations suggest a catabolism of about 500 mg protein per day per chick during the time immediately after hatching. The discrepancy between the above results can perhaps be partly explained against the background of the changes of the protein metabolism of the capercaillie chicks during the first days after hatching.

According to Table 9 a synopsis of the analytical results for the time between the ages of 1 and 2.5 days indicates that during this time the dry weight of the unfed chicks has decreased by an average of 0.090 g. As this difference is not statistically significant, the protein metabolism is discussed without regard to this decrease in the chicks' total dry

Table 9. Comparison of the dry weight and amount of lipids in the body, and the amount of proteins in the yolk sac and liver in unfed capercaillie chicks between the ages of 1 and 2.5 days.

Compared components	At age of 1 day (g)	At age of 2.5 days (g)	Difference (g)
Dry weight of body (yolk sac and liver not included)	7.190	7.100	- 0.090
Body lipids (yolk sac and liver not included)	1.899	1.671	- 0.228
Liver proteins	0.159	0.184	+ 0.025
Yolk sac proteins	0.784	0.283	- 0.501

weight. However, the amount of lipids in the body has decreased by 0.228 g ($t=2.56$, $f=26$, $p<0.01$), which means that a corresponding increase of the other dry substance in the body must have taken place, and in addition to this there is an increase in the liver proteins of 0.025 g ($t=2.88$, $f=27$, $p<0.005$). Altogether there is 0.253 g (0.228 + 0.025) of dry substance which, with the exception of a small storage of inorganic material, must for the main part be derived from the proteins of the yolk. These have during the same time decreased by 0.501 g, which means that more than 0.248 g (0.501-0.253) of protein has been used for the satisfaction of the energy requirements of the body. This signifies a considerable increase in protein catabolism compared with the first day of life. When FRIDERICIA, in his analyses referred to earlier, determined the mean value of the excretion of uric acid during the first 2-3 days after the hatching of domestic chicks he did not know that the magnitude of the protein catabolism changes between the first and second day of life. For this reason his value appears too high to be referred to the first day of life, and too low to be referred to the second day. The high values obtained by ROMENSKY for protein catabolism can possibly be explained by the fact that this author used chicks that were not newly hatched (see page 27). In spite of this possible explanation his values appear under all circumstances too high.

In accordance with the bases of the calculations which have been applied above the capacity of the protein catabolism in the starving capercaillie chicks was determined also between the ages of 2.5 and

Table 10. Comparison of the dry weight and amount of lipids in the body, and the amount of proteins in the yolk sac and liver in unfed capercaillie chicks between the ages of 2.5 and 4.5 days.

Compared components	At age of 2.5 days (g)	At age of 4.5 days (g)	Difference (g)
Dry weight of body (yolk sac and liver not included)	7.100	6.270	- 0.830
Body lipids (yolk sac and liver not included)	1.671	0.826	- 0.845
Liver proteins	0.184	0.136	- 0.048
Yolk sac proteins	0.283	0.054	- 0.229

4.5 days (Table 10). During this period the dry weight of the capercaillie chicks falls by 0.830 g, while the amount of lipids in the body decreases simultaneously by 0.845 g. The difference between these two values is negligible (0.015 g), and consequently no substantial increase of the protein content of the body seems to take place during this period. On the other hand the amount of proteins in the liver decreases by 0.048 g ($t=5.56$, $f=25$, $p<0.0005$), and during the same time 0.229 g protein disappears from the yolk. Thus in the starving capercaillie chicks about 0.277 g ($0.048+0.229$) of proteins is mobilized between the ages of 2.5 and 4.5 days. This is mainly used to maintain catabolism.

Thus towards the end of the observation time the protein balance of the body is displaced towards the negative side, the protein catabolism exceeding the supply of protein from the yolk. Between 4.5 and a full 5 days of age the decrease in the amount of proteins in body, liver, and yolk is, however, not statistically established. This experimental period was obviously too short to give a significant result concerning the protein metabolism of the chicks.

Starting from the above result the following points can be added to what has been stated above about the protein metabolism in starving capercaillie chicks:

3) During the chicks' second day of life a marked increase of the protein catabolism takes place. In unfed capercaillie chicks about half the proteins resorbed from the yolk at this time seems to be catabolized.

4) Between the ages of 2.5 and 4.5 days the protein catabolism is

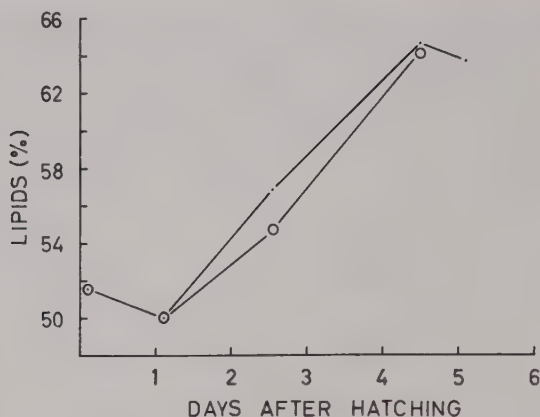


Fig. 12. Percentage of lipids in the dry weight of the yolk sac in the groups of fed (O) and unfed (·) capercaillie chicks.

of about the same magnitude as the protein resorption from the yolk during the same time. The proteins of the liver decrease slightly and the storage in the body is quite insignificant.

5. *Lipids.*

The main part of the energy used for the development of the domestic chick embryo is obtained by catabolism of the lipids of the yolk (cf. page 31). In consequence the lipid concentration falls, and the protein concentration rises in the yolk during incubation. About 32% of the yolk of the egg of the domestic hen consists of lipids, and ROMANOFF (71) states the lipid concentration in the yolk sac of the embryo of the domestic chick at the age of 20 days to be 20.35%. According to unpublished determinations of my own the lipid concentration in the yolk sac of newly hatched domestic chicks amounts on the average to $21.80 \pm 0.81\%$ ($n=8$).¹ The corresponding value for the capercaillie chicks is $29.12 \pm 0.67\%$ ($n=20$). Thus the lipid concentration of the yolk is considerably higher in the capercaillie chicks. On the other hand, as has already been established earlier, the amount of yolk as a percentage of the body weight is considerably higher in domestic chicks.

The absolute quantity of lipids in the yolk sac of the newly hatched capercaillie chick amounts on the average to 1.832 g, and in the fed

¹ Minor differences might exist between different races of domestic fowl.

individuals its decrease seems on the whole to keep pace with the decrease in wet weight of this organ (Table 7). This is also the case in the unfed chicks up to the age of 2.5 days after which point of time the rapidly increasing water concentration in the yolk of these chicks causes a decrease of the lipid concentration. If on the other hand the amount of lipids is expressed in relation to the dry weight of the yolk sac, another picture of the utilization of the yolk fat is obtained (Fig. 12). During the chicks' first day of life the decrease of the lipid in the yolk goes on at about the same rate as its dry weight decreases. After this the relative rate at which the proteins and carbohydrates disappear from the yolk increases. This is reflected in a considerable increase of the lipid concentration per dry weight.

C. The Liver

1. Wet Weight and Dry Substance.

During the time immediately after hatching both the wet and dry weight of the liver increase (like the dry weight of the body) although the chicks do not take any food (Fig. 13). Unpublished investigations of my own have shown this to be the case also in domestic chickens. According to the literature which has been available to the author this fact has not received any attention previously. ENTENMAN, LORENZ, and CHAIKOFF (15), in a work on the lipid concentration in certain tissues in domestic chicks, have reproduced a growth curve of the wet weight of the liver according to which the weight is constant during the first

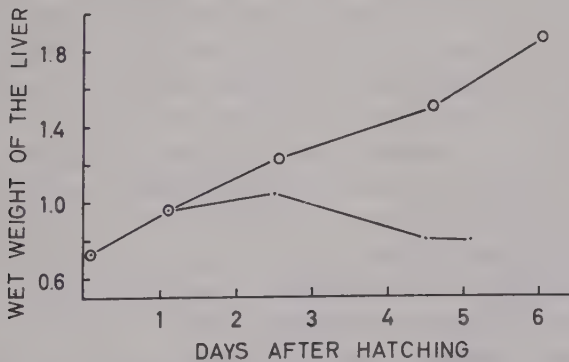


Fig. 13. The wet weight in gram of the liver in the groups of fed (○) and unfed (·) caper-caillie chicks.

Table 11. Wet weight, dry weight, and percentage of dry substance in the liver, and the relation between the wet weights of this organ and of the body (yolk sac not included) in the fed and unfed capercaillie chicks.

Experimental group	Wet weight (g)	n	Dry weight (%)	Dry substance (g)	n	Liver weight in per cent of body weight (yolk sac not included)	n
0.02 S	0.730 ± 0.011	21	0.243 ± 0.005	33.24 ± 0.35	20	2.32 ± 0.37	21
1.02 S	0.961 ± 0.017	18	0.330 ± 0.006	34.00 ± 0.52	14	3.04 ± 0.06	18
2.13 S	1.045 ± 0.039	14	0.378 ± 0.011	36.34 ± 0.69	14	3.30 ± 0.11	14
4.12 S	0.803 ± 0.029	16	0.304 ± 0.011	37.87 ± 0.78	14	2.92 ± 0.13	14
5.02 S	0.797 ± 0.033	16	0.293 ± 0.011	37.19 ± 0.77	15	2.83 ± 0.12	13
2.13 F	1.228 ± 0.040	13	0.431 ± 0.012	35.20 ± 0.50	13	3.53 ± 0.08	13
4.14 F	1.488 ± 0.076	15	0.455 ± 0.026	31.87 ± 0.47	12	3.59 ± 0.12	14
6.01 F	1.866 ± 0.091	14	0.564 ± 0.036	30.18 ± 0.37	13	3.87 ± 0.13	14

two days of life. That an increase in the weight of the liver has not been shown in the investigations referred to is probably due to the circumstance that some of the chicks have not been quite newly hatched at the beginning of the experiments, since it appears from their work that all the chicks have been removed from the incubators on the 22nd day after the beginning of incubation. This must mean that at this time some individuals have in fact been more than a day old.

The wet weight of the liver of the capercaillie chicks increases during the first day by 31 to 32% (Table 11). As a matter of fact the rate of growth is of the same magnitude during this period as in fed chicks of a higher age, and the dry weight of the liver increases even somewhat faster than its wet weight. However, the growth of the liver becomes gradually slower in the unfed chicks, and from the age of 2.5 days, when the main part of the yolk has been resorbed, and onwards, a decrease of the weight of the liver sets in. In the fed chicks the growth of the liver proceeds continuously.

During the latter part of the embryonic development of the domestic chick the relation between the weights of the liver and the body is relatively constant, and consequently the growth goes on in parallel (94). Between the 13th and 20th day of incubation the liver constitutes a little less than 2.5% of the wet weight of the domestic chick embryo

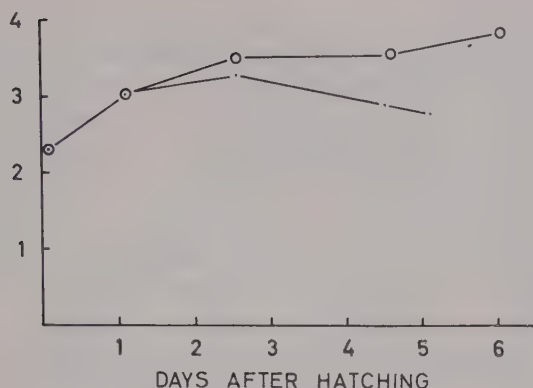


Fig. 14. Wet weight of the liver in percentage of the wet weight of the body (yolk sac not included) in the groups of fed (○) and unfed (·) capercaillie chicks.

(yolk deducted), and in the newly hatched capercaillie chick the corresponding value is 2.32 ± 0.37 (Table 11). However, during the first 2.5 days of life this figure rises considerably in unfed as well as in fed individuals, which means that after hatching the liver grows more rapidly than the rest of the body (Fig. 14). This continues in the fed chicks also between 2.5 and 6 days of age, although at a somewhat slower rate. During this period the liver increases from 3.53 to 3.87% of the body weight ($t=2.26$, $f=25$, $p<0.025$). Against the background of these rising values it is of interest to notice that gradually a substantial decrease in the portion of liver in the body weight of the capercaillie begins. A small number of specimens have been examined, and according to these the liver amounts to about 2.3% of the body weight at the age of 3 months (4 specimens). The corresponding value for birds more than 1 year old (4 specimens) has dropped to an average of 1.4%.

In the starving chicks the weight ratio of liver to body decreases after the age of 2.5 days from 3.30 to 2.83% ($t=2.96$, $f=25$, $p<0.005$). It does, however, not reach the same low value it had at hatching.

The problem of the changes in the water concentration of the liver of starving animals is not new, and has been the subject of several investigations. In spite of this the earlier opinions concerning this question have differed even with regard to the same species, since the water concentration of the liver is influenced also by individual differences as well as by a large number of other factors, e.g. species, age,

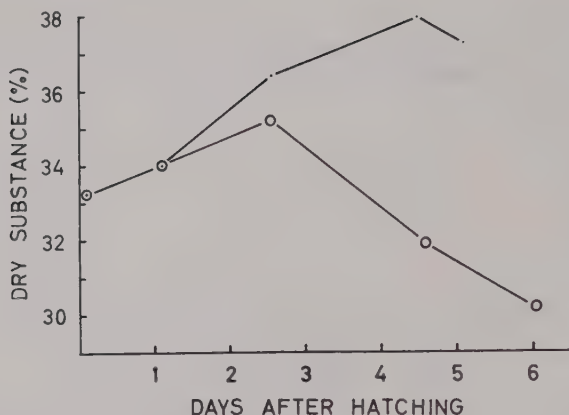


Fig. 15. Percentage of dry substance in the liver in the groups of fed (○) and unfed (·) capercaillie chicks.

size, state of nutrition, and condition at the start of the experiment, the length of the starvation period, etc.

The experiments with the capercaillie chicks satisfy high requirements for uniformity both in regard to material and experimental conditions, and they ought therefore to supply reliable information on the changes in the water concentration of the liver in fed and in starving chicks. At hatching the dry substance amounts to 33.24% of the wet weight of the liver, and later this value increases in the unfed chicks to 37.87% at the age of 4.5 days, when the analyses indicate a small, not significant drop (Fig. 15). In the fed chicks the percentage of dry substance in the liver is increased during the first 2.5 days ($t = 3.24$, $f = 31$, $p < 0.005$). After this, however, there is a strong downward trend, with a decrease of 5 units up to the age of 6 days.

A considerable amount of water is known to accompany the proteins in the liver, FENN and HAEGE (19) reporting up to 3.58 g water per g of protein. Since the changes in the concentrations of carbohydrates and lipids in the liver are relatively small during the first 2.5 days after the hatching, the increase during this period of the concentration of proteins in the liver especially of unfed chicks (Table 12) ought to bring about an increase in the concentration of water which on the contrary decreases in both fed and unfed individuals. In order to obtain an idea of the factors that govern this unexpected relation between the contents of proteins and water we have to fit this problem

into a wider context. The first thing to offer itself is the infiltration of fluids into the body of the chicks that takes place towards the end of the incubation, and the desiccation of the tissues following upon it (cf. p. 20). In analogy to these conditions in the remainder of the body the changes in the water concentration of the liver after the hatching would indicate that also this organ is influenced by the mentioned infiltration before the hatching and in consequence it becomes subject to a desiccation of the tissues during the first days of life of the chicks. In the liver the reduction in the water concentration occurs admittedly somewhat slower than in the rest of the body, but seems on the other hand to be extended over a somewhat longer period.

However, to all appearances about the age of 2.5 days other factors begin to operate. These cause the percentage of dry substance in the liver to drop in the fed chicks, while it continues to rise in the unfed ones. The agreement between Figs. 15 and 19 in the parts which apply after the age of 2.5 days indicates a close connection between the lipid concentration and the percentage of dry substance. The increase of the lipid concentration brings about a decrease in the water concentration, and *vice versa*. These observations are in agreement with the previously established circumstance that the deposition of fat in the liver of rats is not accompanied by any appreciable amount of water (39, 19, 52).

On the other hand the changes in the contents of proteins and carbohydrates in the liver do not seem to exhibit variations of a magnitude sufficient to account for the reported change in the water contents of this organ. Concerning the content of carbohydrates FENN and HÆGE, e.g., state: "The total liver weight increases as its glycogen content increases, as if water and glycogen had been added to what was there previously without replacing any other constituents."

2. Carbohydrates.

It is a well known fact that the main part of the carbohydrates of the body exists as glycogen in the liver and muscles, while the proportion is small in other organs. Of these two main components the muscle glycogen is relatively stable. It decreases, however, substantially during prolonged muscular work (cf. below), and a decrease is also seen during starvation, although the glycogen in the cardiac muscles is unique in this respect, and remains constant or even increases during the starvation period (43, 50, 10, 45, 91). In comparison with the muscle glycogen

Table 12. The amount of carbohydrates, proteins, and lipids in the liver of the fed and unfed capercaillie chicks.

Experimental group	Carbohydrates			Proteins			Lipids		
	mg	% of the wet weight of the liver	n	mg	% of the wet weight of the liver	n	mg	% of the wet weight of the liver	n
0.02 S	9.4 ± 0.4	1.28 ± 0.05	21	107 ± 2	14.69 ± 0.13	18	128 ± 3	17.60 ± 0.30	21
1.02 S	13.8 ± 0.9	1.42 ± 0.08	16	159 ± 4	16.49 ± 0.23	15	162 ± 4	16.99 ± 0.47	17
2.13 S	14.0 ± 1.7	1.33 ± 0.12	13	184 ± 8	17.57 ± 0.30	14	182 ± 5	17.57 ± 0.57	14
4.12 S	8.5 ± 0.4	1.04 ± 0.04	14	136 ± 4	17.04 ± 0.36	13	155 ± 6	19.47 ± 0.56	15
5.02 S	7.5 ± 0.2	0.95 ± 0.04	16	129 ± 4	16.50 ± 0.43	15	150 ± 8	18.80 ± 0.70	15
2.13 F	32.8 ± 5.0	2.58 ± 0.37	11	193 ± 7	15.82 ± 0.26	11	206 ± 6	16.96 ± 0.58	12
4.14 F	48.4 ± 5.8	3.32 ± 0.27	12	218 ± 14	15.51 ± 0.53	11	168 ± 8	11.82 ± 0.42	13
6.01 F	102.5 ± 17.1	5.14 ± 0.66	12	279 ± 17	14.74 ± 0.55	12	169 ± 5	9.23 ± 0.31	14

the liver glycogen is labile, and can vary within wide limits under different experimental conditions. Therefore it was natural to concentrate interest on the liver and the yolk sac during the consideration of the carbohydrates in this work.

During the last day of incubation the amount of glycogen decreases in the growing embryo (36, 54, 55, 95), probably owing to the intense muscular work for the breaking of the egg shell. There exist also many proofs of an increased activity in the embryo during this stage, e.g. an increased CO₂ production (63) and an increased body temperature (18, 46). Also the glycogen store in the liver decreases markedly owing to the great stress during hatching (94). No similar decrease occurs on the other hand in the mammals, but the glycogen concentration in the liver even increases most rapidly towards the end of the foetal stage (48, 47, 86, 11, 24). According to my opinion this fact must be viewed against the background of the passiveness of the mammalian foetus during the birth act in comparison with the activity of the bird embryo.

Two hours after hatching the liver of the capercaillie chicks contains 9.4 mg carbohydrates (Table 12), and it can be assumed that this value is lower immediately after hatching, before the period of rest and sleep which is characteristic of the time, when the drying of the plumage

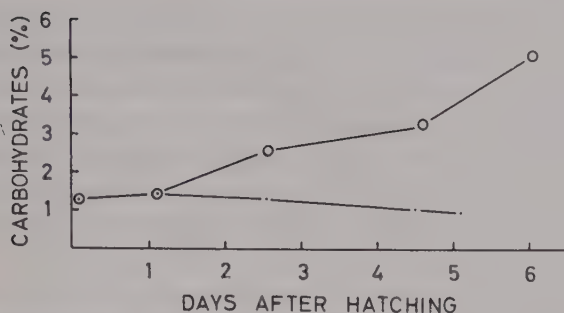


Fig. 16. Percentage of carbohydrates in the wet weight of the liver in the groups of fed (O) and unfed (·) capercaillie chicks.

is going on (cf. Fig. 2). The investigations also show that the total amount of carbohydrates in the liver increases during the first 2.5 days, even in chicks which have not been fed. This is directly opposed to the view which has been enounced previously by WLADIMIROW (94): "Nach dem Herauskriechen aus dem Ei verringert sich der Glykogenhalt in der Leber besonders wenn das Küchlein hungert." His small number of analyses are, however, not extended beyond the specific hatching day, i.e. for domestic chicks 21 days after the beginning of incubation. Perhaps his observation of the considerable glycogen decrease during incubation induced him to make the premature assumption that this decrease is continued if the chicks are not fed. The analyses presented here show that during the first day of life the quantity of carbohydrates in the liver of the starving capercaillie chick increases from 9.4 to 13.8 mg ($t=4.27$, $f=35$, $p<0.0005$). The increase, which thus is largest immediately after hatching, is probably connected with the rapid metabolism of the yolk during this period. During prolonged starvation the quantity of carbohydrates in the liver drops below the value at hatching, the decrease amounting to nearly 50% between the ages of 2.5 and 5 days.

However, it is clear that the percentage of carbohydrates in the liver of starving chicks varies considerably less between different age groups than the absolute quantity (Table 12 and Fig. 16). This is due to the fact that also the weight of the liver shows a marked increase during the first 2.5 days of life, after which its weight decreases again.

The fed capercaillie chicks show a surprisingly rapid increase of the

carbohydrate store in the liver. Already at the age of 2.5 days this amounts to about 33 mg, and at the age of 6 days the amount of carbohydrates in the liver has increased by more than 10 times (Table 12). A corresponding, although on account of the growth of the liver less marked increase is also seen in the percentage of carbohydrates which increases from 1.28% at hatching to 5.14% 6 days later (Fig. 16). The rise of the curve is especially marked between the ages of 4.5 and 6 days.

Also in fed domestic chicks the glycogen concentration of the liver increases markedly during the days immediately after hatching (14). After this a decrease sets in again, and it is conceivable that a similar situation could also have been shown in tetraonids, if the analyses had been extended to include older individuals as well.

A factor which also ought to be brought up for discussion in an investigation of this sort, where the amount of liver glycogen in different experimental groups is compared, is the so-called diurnal rhythm of the liver. Already in 1927 FORSGREN showed that the concentration of glycogen in the liver of rabbits is subjected to diurnal variations, and later such variations were established in our most common laboratory animals (cf. e.g. 96, 31, 82, 32). According to SECKEL and KATO (79), however, the diurnal rhythm is not developed in rats until the age of 2–3 weeks. On the other hand, PETRÉN, SOLLBERGER and ELFVIN in the series of investigations partly carried out in collaboration (1953–1955), established that the liver glycogen rhythm is developed already in 5 day old domestic chicks. In these the glycogen concentration has high values during the day, with a maximum about 5 p.m., and low values during the night, with a minimum value about 3 a.m. However, according to these investigators the liver glycogen seems to vary more rapidly during the embryonic development, and during the days immediately before and after hatching there occurs a gradual change to the slower rhythm. Nevertheless PETRÉN (64) says about the embryonic stages: "Es ist nicht ohne weiteres klar, ob die gefundenen Kleinrhythmen wirkliche Equivalenten der fertigen Tagesrhythmen darstellen oder ob sie dem statistischen Zufall zuzuschreiben sind."

The cause of the glycogen variations is still not satisfactorily explained, but both endogenous and exogenous factors seem to be at work. A number of experiments carried out by the same investigators, proved the very marked influence of exogenous factors, a reversal of the feeding times, or of the lighting from day to night bringing about a corre-

sponding reversal of the diurnal rhythm of the liver glycogen. This was particularly striking with regard to the feeding.

A survey of my own experimental material from capercaillie chicks with regard to the glycogen concentration of the liver in individuals which had been killed at different times of the day and night gave, however, no indication of a diurnal rhythm. This fact is not so surprising concerning the unfed chicks, the glycogen concentration of which is moreover characterized by relatively small individual variations. Also the liver of domestic chicks is without the glycogen rhythm, if they are starved for a whole day at the age of 5 days (14). However, it seems more remarkable that it has not been possible to establish the existence of a diurnal rhythm in the fed capercaillie chicks, especially bearing in mind that the two species compared are relatively closely related. Yet it is conceivable, against the background of the great influence of the exogenous factors on the diurnal rhythm, that the continuous feeding of the young capercaillie chicks and the rather constant lighting conditions in the experiment (only a couple of hours around midnight are dark) can have counteracted the appearance of marked diurnal variations. However, the experimental material is too limited to allow far-reaching conclusions about this problem.

3. Proteins.

Proteins are not stored in the animal body to the same extent as lipids. There seems, however, to exist a certain reserve which can be mobilized, when the supply of proteins is insufficient. It has not been possible to prove that any particular protein forms part in this reserve, even if SCHULTZ and VARS (78) have found that the labile proteins can differ from the stable ones in regard to composition. On the other hand it is known that certain tissues such as blood plasma, kidneys, and above all the liver (1, 2) contain more labile proteins than other tissues. Consequently these organs have the largest protein loss during starvation or on a low protein diet.

The proteins of the liver have been the subject of a large number of investigations. CAMPBELL and KOSTERLITZ (6) have further elaborated the idea of a labile cytoplasm in the liver. They establish that at least 60% of the nitrogen, which is excreted in the urine during the first days after rats have been put on a protein free diet, is derived from the liver. LAGERSTEDT (42) has proved in a detailed work that basophilic inclusions in the liver cytoplasm represent the protein that is lost

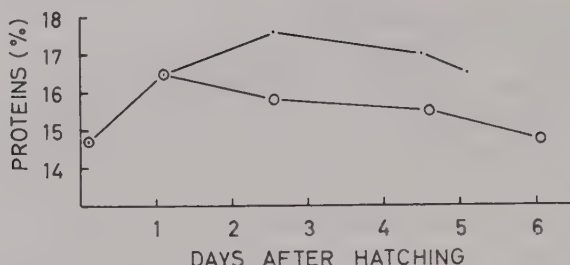


Fig. 17. Percentage of proteins in the wet weight of the liver in the groups of fed (○) and unfed (·) capercaillie chicks.

during starvation or on a protein free diet. He found that 5 days' starvation bring about a decrease of about 40% in the total amount of nitrogen in the liver of rats.

The amount of protein in the liver of unfed capercaillie chicks increases from 107 mg at hatching to 184 mg 2.5 days later (Table 12). During continued starvation the amount of protein decreases by roughly 30% between the ages of 2.5 and 5 days, compared with the decrease of 40% found by LAGERSTEDT in rats in his starvation experiments extended over 5 days. However, in contrast to the carbohydrates the amount of proteins in the liver of starving chicks does not fall below the value at hatching.

The protein concentration of the liver of unfed capercaillie chicks increases and decreases in about the same manner as the total amount of proteins (Fig. 17). The changes are however less conspicuous, since the wet weight of the liver shows, like the protein, a maximum at the age of 2.5 days. Yet the increase of the protein concentration of the liver from 14.69 to 16.49% ($t=3.71$, $f=28$, $p<0.0005$) during the first day of life is surprisingly large, and it seems plausible to assume that this protein increase implies primarily an addition to the protein reserve of the liver. In other words this assumption could mean that the protein reserve of the liver is partly used up during the strenuous hatching stage, as has been established earlier to be the case with the glycogen reserve. After the age of 2.5 days the protein concentration drops from 17.57 to 16.50% ($t=2.06$, $f=27$, $p<0.025$).

In the fed chicks the amount of proteins in the liver increases with increasing age (Table 12). The protein concentration also shows a marked increase during the first day after hatching, as has been estab-

lished above, but subsequently a continuous decrease goes on during the remaining time of the observations. Also the lipid concentration of the liver decreases in the fed chicks during the latter part of the observation period according to what is established below (see page 49). However, during the same time considerable increases in the concentration of carbohydrates as well as of water correspond to these decreases.

4. *Lipids.*

As was the case with glycogen the amount of lipids in the liver can vary within wide limits, even in individuals within the same species. Experiments show that the food supply, and then not merely the amount but perhaps above all the nature of the food consumed is of essential importance for the composition and quantity of lipids in the liver.

Already in 1940 ENTENMAN, LORENZ, and CHAIKOFF established that the liver of newly hatched domestic chicks contains very large amounts of lipids. One of their experiments gave values between 13 and 14.7% of the wet weight of the liver, and in another experiment they obtained a figure as high as 23%. According to their analyses up to 48% of these amounts of lipids or between 5.9 and 9.7% of the wet weight of the liver are made up of cholesterol of which by far the largest part (about 90%) occurs in esterified form.

The liver of the capercaillie chicks at hatching also contains unexpectedly large accumulations of lipids. In the present investigation these amount to 17.60% of the wet weight of the liver. This value is so high that one can simply speak of a physiological "fatty liver".

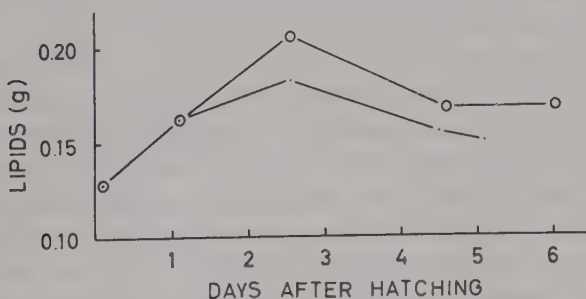


Fig. 18. The amount of lipids in the liver in the groups of fed (O) and unfed (·) capercaillie chicks.

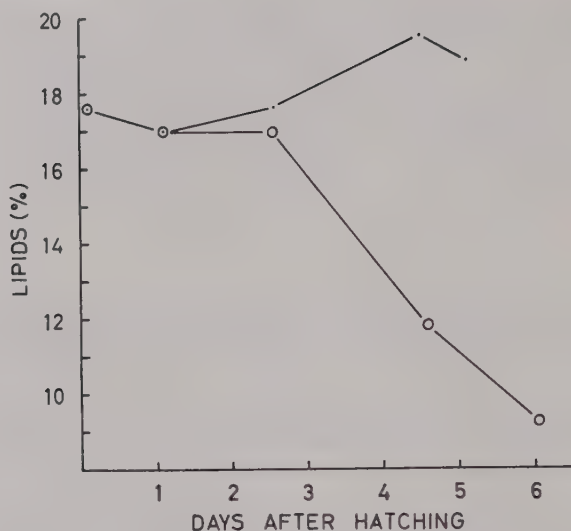


Fig. 19. Percentage of lipids in the wet weight of the liver in the groups of fed (○) and unfed (·) capercaillie chicks.

The total amount of lipids in the liver of unfed capercaillie chicks increases from 128 mg at hatching to 182 mg 2.5 days later, an increase of roughly 42% (Table 12). During continued starvation it drops to 150 mg at an age of 5 days ($t=3.27$, $f=27$, $p<0.005$), but does not reach down to the value at hatching. This finding contradicts the supposition by DUMM and LEVY (12) that the accumulation of lipids in the chicks liver prior to hatching serves as a source of energy for the young animal during its first few hours of independent existence.—The lipid concentration of the liver fluctuates in another way than the absolute amount of lipid (cf. Figs. 18 and 19).

The decrease which according to Fig. 19 takes place during the first day of life is not statistically significant, but after this the lipid concentration in the liver of the unfed chicks increases continuously up to the age of 4.5 days, when the tendency becomes again falling. ENTENMAN, LORENZ, and CHAIKOFF on the other hand obtained in their analyses of domestic chicks a small increase of the lipid concentration of the liver during the first day after hatching. If this increase is significant, which cannot be concluded from the particulars given, then there either exists in this respect a certain difference between domestic chickens and capercaillie, or the discrepancy between the two results

is due to some of the domestic chicks used, possibly being, as has already been mentioned earlier, not quite newly hatched at the start of the experiments (cf. page 38).

It is known that starvation can cause a very large accumulation of lipids in the liver. In certain laboratory animals this lipid increase is less conspicuous, and in some cases the changes are so small that their demonstration is difficult. With regard to the very high lipid concentration in the liver of capercaillie chicks, which is found already at hatching, it is not surprising that the lipid concentration shows a relatively moderate increase during the following period of starvation. This increase is probably connected with a continuing mobilization of the fat depots of the body, and seems to be dependant on a metabolic disturbance.

In fed capercaillie chicks the amount of lipids in the liver increases from 128 mg at hatching to 206 mg 2.5 days later. On account of the marked growth of the liver this lipid addition does, however, not correspond to an increase in the lipid concentration (Fig. 19). Between the ages of 2.5 and 4.5 days the absolute quantity of lipids in the liver of the fed chicks decreases by 38 mg ($t = 3.92$, $f = 23$, $p < 0.0005$), although the weight of the organ increases by 260 mg. This causes the lipid concentration to drop rapidly during this period. According to ENTENMAN, LORENZ, and CHAIKOFF the same is the case also in the liver of fed domestic chicks. This decrease continues in capercaillie chicks at least up to the age of 6 days.

The marked decrease of the lipid concentration of the liver in fed chicks coincides in a striking way with the age, when they have absorbed the main part of the yolk, and to a larger extent begin to take food from outside. It can be assumed that the change from the yolk diet, rich in cholesterol and other lipids, to a diet with a higher protein concentration, is actually the immediate reason for the decreasing lipid concentration in the liver. (Concerning the influence of the diet on the contents of lipids in the liver cf. e.g. 3, 49, 92, 9, 66.) From a comparison of the analytical results in fed and unfed capercaillie chicks it is therefore clear that the lipid concentration of the liver between 2.5 and 6 days of age is closely connected with the nutritional state of the chicks. As ENTENMAN, LORENZ, and CHAIKOFF also point out, the origin of the unexpectedly high lipid concentration in the liver of the chicks at hatching could possibly also be connected with the food substances which are metabolized during embryonic development.

D. The Fat Depots of the Body

Owing to the increasing rate of mobilization of the lipids of the egg yolk the amount of lipids in the growing embryo increases rapidly towards the end of incubation (54, 71). At hatching the lipids in the body of the capercaillie chick (yolk sac and liver not included) amount to roughly 1.8 g, or to about the same amount as remains in the yolk sac at this time (Tables 7 and 13). A large part exists as subcutaneous fat in the form of larger or smaller deposits in certain parts of the body. Such accumulations occur primarily on the neck and breast of the capercaillie chicks, but not on the back of the body (Fig. 20 a). Domestic chicks also show "organ-like" fat deposits associated with the skin (44). These even seem to maintain a definite form in the fully grown birds.

The absolute quantity of lipids in the body undergoes no significant change during the first day of life of the capercaillie chicks in my experiments (Fig. 21). As the dry weight of the body on the other hand increases substantially during this time (cf. Fig. 4), the lipid concentration will begin to decrease from hatching onwards (Fig. 22). At an age of 1 day a utilization of the fat depots of the body begins in the unfed chicks. This reaches its greatest intensity after the age of 2.5 days, when the main part of the yolk sac is already resorbed. It is primarily the considerable fat deposits connected with the skin that are substantially

Table 13. The amount of lipids in the body of the fed and unfed capercaillie chicks (yolk sac and liver not included).

Experimental group	Lipids in the body (yolk sac and liver not included)			
	g	n	% of the dry weight of the body	n
0.02 S	1.798 ± 0.048	20	27.60 ± 0.49	20
1.02 S	1.899 ± 0.053	16	26.38 ± 0.49	16
2.13 S	1.671 ± 0.071	12	23.07 ± 0.82	11
4.12 S	0.826 ± 0.030	14	13.17 ± 0.43	14
5.02 S	0.662 ± 0.012	15	11.07 ± 0.21	14
2.13 F	1.964 ± 0.101	12	24.30 ± 0.71	12
4.14 F	1.943 ± 0.145	13	20.81 ± 1.02	13
6.01 F	2.277 ± 0.141	12	20.73 ± 0.71	12



a



b

Fig. 20. Skin of capercaillie chicks. *a*. Newly hatched chick. *b*. 5 days old chick which has not been fed. The skin is cut open on the ventral side of the chicks. Note the great differences with regard to the subcutaneous fat. Photo N. Höglund-V. Marcström.

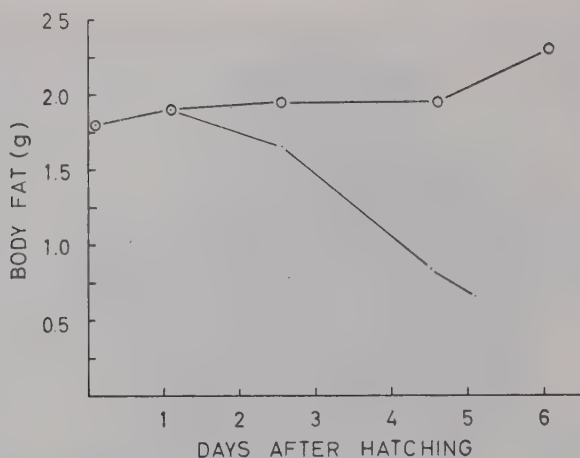


Fig. 21. The amount of body fat in the groups of fed (○) and unfed (·) capercaillie chicks.

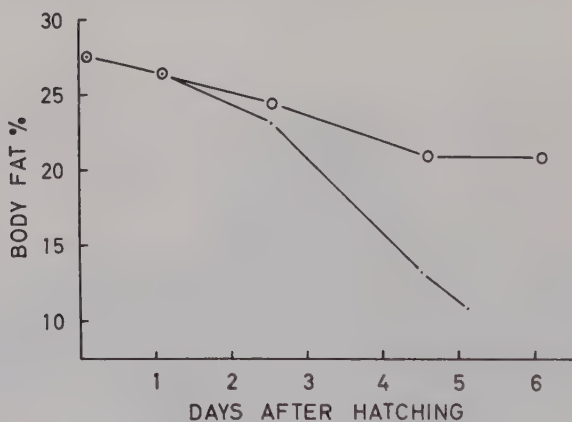


Fig. 22. Percentage of fat in the reduced dry weight of the body (yolk sac and liver not included) in the groups of fed (○) and unfed (·) capercaillie chicks.

reduced during this stage (Fig. 20 *b*). Thus between the ages of 2.5 and 5 days the lipid concentration falls from fully 23 to 11% of the dry weight of the capercaillie chicks. This implies a decrease in the total quantity of lipids of roughly 60%. The importance of subcutaneous fat in temperature regulation is self-evident, even if most of it is not distributed as an even layer over the whole body. Considerable amounts

Table 14. The amount of lipids and cholesterol in newly hatched and 4 days old, fed and unfed *domestic* chicks.

Experimental group	Number of chicks	Body lipids (yolk sac and liver not included) (g)	Cholesterol in the body (yolk sac and liver not included)	
			mg	% of the amount of body fat
0 S	6	2.092	208	9.93
4 S	6	1.106	182	16.47
4 F	6	2.235	206	9.21

of lipids in the body are, however, bound in such a way that they cannot be mobilized, even if the chicks are severely starved.

Surprisingly enough the quantity of lipids in the body of the fed capercaillie chicks is found to remain almost constant between the ages of 1 and 4.5 days, although the dry weight of the body (yolk sac and liver not included) increases from 7.2 to 9.2 g in round numbers. As a consequence the lipid concentration drops from 26.38 to 20.81 % during this period. Conditions are thus comparable to what has been established above for the liver.

For the liver of domestic chicks it is known that the decrease of the lipid concentration after hatching implies among other things that the main part of the esterified cholesterol is utilized (15). In order to get an idea also of what happens with the cholesterol in the other parts of the body during the corresponding period, the author has carried out analyses of newly hatched and 4 day old, fed and starved, domestic chicks (yolk sac and liver not included). In this case the chicks within each experimental group have not been analysed individually, and so the individual differences are neglected. However, the investigations give a relatively good understanding of the problem set forward.

The results indicate that the absolute quantity of cholesterol is comparatively constant during the first 4 days of life (Table 14). Only in starving individuals does an insignificant decrease occur, although almost 50 % of all the body fat is utilized during the period in question. In this way the proportion of cholesterol in the total quantity of lipids is considerably increased in these individuals.

In conclusion, with regard to cholesterol it can be established that the cholesterol depots of the liver are rapidly reduced after hatching, while the quantity of cholesterol in the rest of the body (yolk sac not included) remains relatively constant during the chicks' first days of life. Cholesterol is supplied to the body not only with the food but also from the yolk sac in connection with its resorption.

V. THE INFLUENCE OF CLIMATE ON REPRODUCTION: DISCUSSION AND FIELD STUDIES

As a basis for a discussion of the influence of the climate on the reproduction of our capercaillie stocks, it would be appropriate to summarize briefly the facts known about the temperature regulation and feeding activity of the chicks and the main outlines of their nutritional physiology.

In the introduction we have already pointed to incomplete temperature regulation of the young capercaillie chicks and to their need of additional warmth from the hen, even in weather conditions which are normal for the season. In favourable weather conditions tentative feeding attempts begin towards the end of the first day of life. During the following days these rapidly become efficient.

The problem, whether maturity or practice has the greatest importance for the development of the chicks' pecking has been discussed by many investigators. SHEPARD and BREED (80) maintained that for domestic chicks the influence of practice is limited mainly to the activity of the first two days, while BIRD (4) argues that maturity is most important during this time. According to CRUZE (8) the pecking is an integration of both maturity and learning, while MOSELEY (53) and PADILLA (59) primarily point to practice as the dominating factor. By forced feeding of domestic chicks, and at the same time keeping them in darkness during a longer or shorter time the latter author could prevent them from developing their feeding activity through practice. Chicks which had been delayed in this way up to 8 days needed the same time to reach a certain efficiency in their pecking as those individuals that had not been delayed. Not until after a couple of days' practice did all the chicks show a rapid improvement of their skill which according to this investigator gradually became more efficient during the following

3-4 days' practice and experience. The longer the delay lasted, the more practice was needed, and the lower the level of skill reached. POULSEN (68), on the other hand, stresses the importance of maturity, and states that two domestic chicks which had been delayed for 4 days attained within a few hours the same skill at pecking as normal chicks. During this period the mechanism which releases the pecking is impressed, i.e. the chicks learn to direct their pecking towards for example grains of corn instead of stones or other objects of the same size.

The reported experiments with domestic chicks are thus by no means in agreement, a fact which to a large extent must be due to differences involved in the experimental conditions and testing methods. Some authors also express different opinion as to how the testing results should be interpreted. As a matter of fact maturity as well as experience and learning ought to have their importance for the attainment of efficient pecking. According to my opinion the influence of physiological maturity is especially marked during the earliest life of the capercaillie chick during which period steadiness of the body and coordination of movements is rapidly improved. The impression of the inborn pecking mechanism and the importance of experience must also be stressed. Experience ought to be of importance to capercaillie chicks, as these, without the aid of the hen, must find their animal and vegetable food on the ground and in the undergrowth.

From the investigations presented here it appears that the capercaillie chicks hatch with considerable food reserves, consisting partly of yolk, the dry matter of which amounts to fully half of the chicks' dry weight, and partly of substantial "fat depots" primarily in association with the skin (Fig. 23). On the other hand, the food substances in the liver which can be mobilized seem to have been consumed during the hard work of hatching.

Yolk resorption takes place most rapidly during the time immediately after hatching, and during the first 2.5 days it covers the main part of the capercaillie chicks' energy requirements. It is able even to increase the dry weight of body and liver to a not inconsiderable extent. It is therefore inappropriate to speak of starving chicks at least during the first day after hatching, especially as food uptake from outside is not begun as a rule until the second day of life. However, after the age of 2.5 days, when the main part of the yolk is already used up, a rapid breaking down of the lipids in the unfed chicks begins, and the chicks die at the age of fully 5 days.

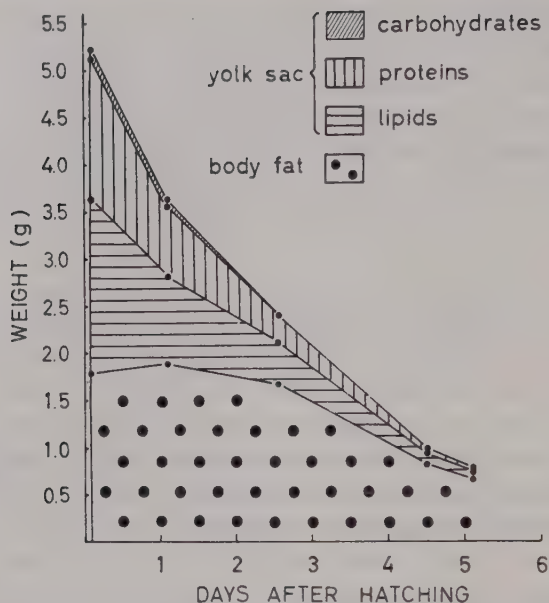


Fig. 23. Resorption of the food substances of the yolk sac and the mobilization of body fat in the unfed capercaillie chicks.

By placing the above factors in relation to each other it is possible to form a good idea of the influence of the climate on the reproduction of our capercaillie stock. If an unfavourable weather situation occurs with rain, wind, and a temperature too low for the chicks during the two to three first days after hatching, then the yolk reserve certainly secures the chicks' energy requirements, but the food supply from outside becomes insufficient, as the chicks are compelled to spend most of the time under the hen. Neither can they therefore improve their searching after food to the same extent as in fine weather. As a consequence part of the fat depots of the body must be used up, and this immediately increases the danger of chilling down.¹ It seems as if the first day of life is the least critical from the point of view of weather conditions, as the capercaillie chicks, as has already been mentioned, under all circumstances need a certain time to dry, and to obtain the necessary steadiness in the legs and coordination of movements. This

¹ According to CARD (7) the body temperature in unfed domestic chicks begins to fall already after the age of 2 days.

first period of time is always spent under or in the immediate neighbourhood of the hen. For securing the survival of the majority of chicks a change to favourable weather conditions must occur about the third day after hatching.

If on the other hand some days of unfavourable weather occur, when the chicks are 2-3 days old, and the main part of the yolk is already resorbed, the situation will rapidly become catastrophic. The fat depots of the body then have to be used in order to cover the immediate energy requirements. Up to half of these lipids, which to a large extent occur as subcutaneous fat and in "organ-like" deposits in association with the skin, is under such circumstances used up between the ages of 2.5 and 4.5 days, hence within 2 days (cf. Table 13). This implies a deterioration of the thermal insulation of the body, and the emaciated chicks, with far from fully developed temperature regulation ability, are subjected to increased risks of infection, they starve to death or succumb in their enfeebled condition to destructive factors of other kinds. It is thus imaginable that the capercaillie chicks which, when freezing, utter a sharp and characteristic plaintive cry more easily become the victims of different predators. However, the role of the predators in this connection ought to be mainly of secondary importance. It ought also to be strongly emphasized in this connection that in my starvation experiments the capercaillie chicks lived in optimal temperature conditions. They were completely protected from the destructive effect on the young organism of large heat losses caused by low temperature, rain, and a wet undergrowth.

During the spring of 1958 the effect of unfavourable climatic factors on the capercaillies' reproduction was studied in special field investigations. Two capercaillie hens with 6 and 9 chicks, respectively, which they themselves had hatched from their own eggs were released into a fenced-in, slightly undulating area of 1.5 hectares with both deciduous and coniferous forest. The undergrowth in the area is in part dense and rich, and the biotope seems capable of offering the capercaillie chicks good feeding possibilities. In one of the broods the individuals were 2 days, and in the other 4 days old at the start of the experiment, and after hatching they had had access to suitable food e.g. bilberry greenery, ant eggs, egg yolk etc. in their outdoor cage. In this way the oldest chicks in particular had got a relatively good start before they were released together with their mother to look after themselves.

The experiment lasted for 7 days, from June 17-23, and as a rule

the area was searched daily, yet with the greatest care so that the two capercaillie broods should not be disturbed. During the first day of the experiment the weather conditions were good with high insolation due to the clear weather. The layer of air nearest the ground especially was strongly heated, and a maximum temperature of 29°C was measured a few centimetres above the sunlit surface, thus at about the level, where the capercaillie chicks were. A temperature of 17.4°C was measured at a height of 1.5 m above the ground. On the second day of the experiment the weather was chilly and cloudy, yet there was no precipitation. All the chicks were alive at noon on this day, which could be established as the two broods stayed near each other in a little glade. On the following 4 days, June 19–22, the weather was colder. The temperature at the 1.5 m level did not exceed 14°C. The high degree of cloudiness and the longer or shorter showers had the effect that the layer of air nearest the surface was not appreciably warmed up by insolation. During these 4 days the rainfall was 27.5, 3.2, 0, and 2.7 mm respectively. Thus on the third day of the experiment the area could not be searched by reason of the risk of dispersing the chicks from the broods during the steady rain, and of in this way exposing them to an unnecessary extent to wet and cold. During the search on the fourth day of the experiment 2, on the fifth day 3, and the sixth day 2 dead chicks were found. When the experiment was terminated on the seventh day only one chick remained in each brood, another one having been removed in very enfeebled condition. This means that a further 5 chicks had succumbed during the time of the experiment, although they could not be recovered within the area, possibly due to the in part dense undergrowth.

The chick which was removed on the last day was almost unconscious from cold, dampness, and starvation, and could not move from the place. After it had been placed under a heating lamp, it came round, began in spite of shyness gradually to eat, and little by little recovered entirely. That this chick could be saved in this way by only warmth and food is a very strong indication that bad weather and not illness was the primary cause of the heavy reduction in the number of capercaillie chicks in the above experiment. The chicks that were recovered dead were also all very emaciated. The amount of body fat varied in 6 of the 7 chicks¹ between 10.45 and 12.35% of their dry weight, with

¹ The seventh chick had been dead for a long time, when it was recovered, and was not analysed.

11.78% as a mean value. The corresponding value in the oldest experimental group of unfed chicks was still a little lower, and amounted to 11.07%. The chicks in the field experiment, which were also exposed to dampness and cold, could probably not withstand starvation to quite the same extent as the experimental animals that lived under optimum temperature conditions.

As an important comparison to the reported field experiment it can be mentioned that two capercaillie hens, which at about the same time hatched their clutches in freedom outside the fenced area, only had 2 chicks each left on the day of the termination of the field experiment. One of these broods consisted in the beginning of 7 chicks which died one after the other, while the original number of chicks in the other brood is not known. The assumption ought to be justified that the prevailing weather conditions contributed to the reduction also of these two capercaillie broods.

Thus it is obvious that the young chicks' dependence on the prevailing weather is of fundamental importance to reproductive capacity of the capercaillies. Some cold and sunless days with rain, wind, and low temperature during the first week of life are a serious threat to successful reproduction.

The field experiments show that also somewhat older chicks succumb for the same reason, and prolonged weather situations of this type are certainly destructive factors of importance even to considerably older individuals that have already survived the first most critical period of life. The increased risk of infection in connection with lowered vitality in the young birds due to dampness can cause a successive thinning out of an originally promising reproduction. This can also happen in outdoor breeding, if the young birds are not kept under cover. Among infectious diseases in the capercaillie toxoplasmosis and coccidiosis can be mentioned (5).

The high temperature, however, that prevails during sunny days in the uppermost ground layers and nearest to the sunlit ground surface (23, 41) is on the other hand particularly beneficial to the young capercaillie chicks. The air temperature at high levels is, however, not affected by insolation to the same high degree. This last-mentioned circumstance is of the greatest importance, and must be clear to anyone who wishes with the help of current meteorological data to compare afterwards the weather and the reproduction result during a certain

year. Attention must thus be paid to the importance of the microclimate, and *all* meteorological data taken into account. On the other hand, the average daily temperature must not be overrated, as a certain average temperature can be the result either of a warm sunny day together with a chilly night or of an overcast less warm day together with an overcast less chilly night. The temperature during the night is of less importance, as the young capercaillie chicks then mainly keep close to the mother's warmth.

In order to estimate more closely the magnitude of the influences which the climate has on the numbers of our tetraonid stocks during the reproduction period, it stands out as an essential condition to acquire a sufficient knowledge of the chicks' food selection. Both plant and animal constituents are however included in their diet, and it seems to be natural that the supply of available insects should also vary with the weather (27, 69).

On the basis of my experimental results there exist, however, already now possibilities to fix the minimum requirements concerning temperature, precipitation, and other meteorological data which are necessary for the capercaillie during the first week of life in order to obtain a good reproduction. This can be done by collecting free-living chicks during hatching periods with more or less favourable weather conditions. With the aid of the weight curves drawn above of the capercaillie chicks' body, liver, and possibly also yolk sac, and the development of the plumage, their age can be determined with great precision. The amount of body fat and the concentration of lipids and glycogen in the liver ought then to give us a good idea of their nutritional state and thereby also of their condition and ability to resist prevailing weather conditions (cf. Fig. 24).—A low concentration of lipids in the body, but a high concentration of lipids in the liver, and at the same time a low glycogen concentration in this organ, in for example 4–5 days old capercaillie chicks indicate that these have on the whole eaten nothing after hatching. The possibilities of their survival under the prevailing conditions are thus almost exhausted, and the weather during the period in question must be regarded as constituting a limiting factor for successful reproduction. If on the other hand the glycogen concentration in the liver in the above example had been high, this would mean that the improvement of the weather, which in this case must have occurred some time before the chicks were caught, has been

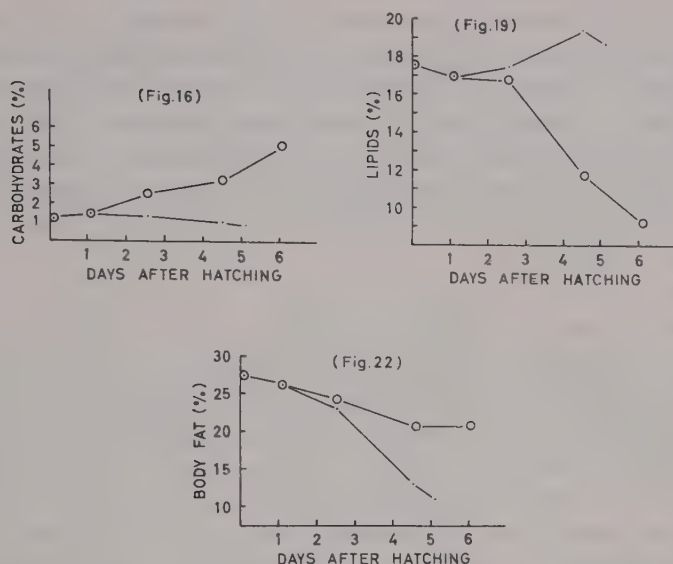


Fig. 24. Juxtaposition of diagrams which among other things show the capercaillie chicks' nutritional state, viz. the amount of body fat and the concentration of carbohydrates and lipids in the liver.

enough to make possible an effective food uptake by the chicks. In this case the more favourable weather situation has on the other hand been of so short duration that a change of the concentration of lipids in the liver and body has not had time to occur. In order to cover different age stages and different types of weather in an investigation of this sort, a considerable amount of experimental material must be procured.

If the above recommended way of determining more exactly the chicks' temperature requirements is extended over a succession of years, and at the same time is combined with parallel indoor starvation experiments in a controlled environment, an idea can also be obtained as to whether or not the chicks' power of resistance and survival capacity varies between different years. According to SIIVONEN (81) such a variation should be due to a difference in quality between the eggs, and this difference should in its turn be connected mainly with the nutrition of the capercaillie hen during the "pre-laying period" which lasts about 3 weeks. According to a hypothesis put forward by SWÄRDSON

(88, 89) the fluctuations of game-birds should possibly be regulated by the botanical rhythm, the food during the winter being in the first place decisive for the condition of the population and also for the reproduction. In either theory the food would constitute the common factor. In one case a winter, in the other a spring with qualitatively or quantitatively poor plant food should cause a poor condition in the mother bird, and thereby also indirectly result in a poor and scanty offspring.

The investigations accounted for here could not confirm these hypotheses. In the years 1955 and 1956 the same number of chicks have been included in the starvation experiments. These individuals have been completely dependent on the food substances stored in the eggs. It has, however, not been possible to establish any difference between the two years in regard to the condition of the chicks and their ability to resist starvation. In contrast the reproduction in the districts from where the experimental material was taken shows great differences during the period in question. In 1955 the reproduction was especially good, but in 1956 particularly poor. Consequently the great difference in the reproduction cannot in this case be attributed to the quality of the eggs and from this to the condition of the chicks at hatching, but must on the contrary have a climatic background. The weather conditions in the districts in question were also much more favourable in the early summer of 1955 than in 1956.

In connection with the above argumentation it is important to recall the fact pointed out previously, viz. that the capercaillie chicks which at hatching possess much yolk seem also to consume more yolk per time unit. This is hardly in favour of the assumption that the size of the yolk sac is of decisive importance for the ability of the chicks to endure starvation, but suggests rather that different individuals stand on an even footing in this respect.

It is also obvious that, in species which like the capercaillie can more than triple their stock during one reproduction period under favourable conditions, some successive years with good reproduction can conspicuously increase the population density. But such species have on the other hand as a rule an average life span which amounts to only one or a few years (cf. e.g. 25, 60). From this follows that the population rapidly decreases, if the reproduction is disturbed during a succession of years. Against the background of these circumstances it is obvious that the meteorological conditions during the reproduction

period can decisively influence the fluctuation of the capercaillie population in our country.

On the basis of the facts presented here it will be necessary for future research in this field to pay special attention to the nutritional ecology of the capercaillie chicks and also chicks of other tetraonids and the great importance of the microclimate for the reproduction.

VI. SUMMARY

In the present investigation into the background of the reproduction of the capercaillie the metabolism of the food reserves has been studied in fed and unfed capercaillie chicks during the first 5-6 days after hatching. In doing so the liver and yolk sac have been analysed for carbohydrates, proteins, and lipids, and the fat depots of the body have been studied. At the same time observations have been made on changes in the dry substance of body, yolk sac, and liver. The dependence of the young chicks on the prevailing weather has been studied in field experiments, and the significance of the food reserves during the first week of life has been discussed in detail. In connection with the investigations the influence of the environment on the reproduction of the capercaillie has been analysed, including a discussion of the conditions before hatching.

The following physiological and ecological results can be especially stressed.

1. Through the intensive yolk resorption the reduced dry weight of the body (yolk sac not included) increases during the first day of life by more than 10 %, although the chicks have not eaten anything during this period.

2. As the result of tissue dehydration the reduced wet weight of the body (yolk sac not included) remains on the contrary constant during the first day of life.

3. A part of the material in the yolk sac passes after hatching via the yolk duct into the intestine.

4. The weight of the yolk sac at hatching is positively correlated with the total body weight of the chicks, this correlation being especially marked among individuals from the same clutch. There exists on the other hand no correlation between the yolk sac and the reduced body weight (without yolk sac).

5. The dry weight of the yolk sac at hatching amounts to a full half of the rest of dry weight of the chick.

6. The resorption of the yolk sac takes place most rapidly immediately after hatching, and at the age of 2.5 days more than three quarters have already been resorbed. Chicks with large yolks at hatching also consume more of it per time units. With regard to the wet weight of the yolk sac it seems that

the intake of food stimulates the resorption. This is, however, not clearly noticeable, if the dry weight is taken as the basis.

7. With increasing age the concentration of water in the yolk sac rises. After the age of 2.5 days this change is more pronounced in the unfed individuals.

8. The concentration of carbohydrates and lipids of the yolk sac (estimated on the wet weight) decreases after the age of 2.5 days in all chicks with the exception of the fed ones in which the concentration of lipids in the yolk sac remains relatively constant all the time. Also the protein concentration of the yolk sac decreases in all chicks, although this decrease begins already after the age of 1 day.

9. A considerable part of the material in the yolk sac is not used to maintain the catabolism of the body, but is instead used for syntheses.

10. During the first day of life the catabolism of lipids dominate entirely just as before hatching. In chicks which do not get any food even later, the catabolism of proteins will however gradually increase, although the catabolism of lipids are dominant all the time.

11. From the moment of hatching both wet and dry weight of the liver increase rapidly, just as the remaining dry weight of the body, although the chicks do not eat anything during their first day of life.

12. The share of the liver in the body weight increases in fed individuals from roughly 2.3% at hatching to 3.9% at the age of 6 days, in order to decrease in fully grown birds as far as 1.4%.

13. The amount of carbohydrates in the liver increases during the time immediately after hatching, although the chicks do not eat anything, while their concentration in this organ remains relatively unaltered. In fed individuals the concentration of carbohydrates increases during the remaining time of the experimental period, while it decreases again in starving individuals.

14. The protein concentration in the liver increases in the beginning, but decreases afterwards towards the end of the experimental period, and it is lower in fed than in unfed individuals.

15. The chicks hatch with a physiological "fatty liver" with a concentration of lipids which remains relatively constant up to the age of 2.5 days. Afterwards the concentration of lipids increases still further in starving individuals, while it decreases substantially in fed individuals.

16. Changes in the concentration of lipids in the liver after hatching are connected in fed chicks with the change from yolk resorption to food uptake on their own. In unfed individuals they are connected with the increasing catabolism of the fat depots of the body.

17. There is a connection between the contents of lipids and the content of water in the liver. After the age of 2.5 days an increase in the percentage of lipids indicates a decrease in the percentage of water and vice versa. On

the contrary neither the concentration of proteins or carbohydrates seems to be responsible for the reported changes in the water of the liver.

18. At hatching the liver does not contain any food substances that can be mobilized, and its dry weight is 20 % higher at the end of the starvation period than at hatching.

19. A considerable part of the fat deposits of the body at hatching exists as insulating subcutaneous fat. This fat is rapidly used up, if the chicks are exposed to starvation after the resorption of the yolk sac.

20. In contrast to the conditions in the liver the amount of cholesterol in the rest of the body does not seem to be appreciably reduced during the chicks' first day of life.

21. With regard to the number of eggs per mature hen or the fertility and hatchability of the eggs the reproduction up to hatching does not seem to show variations between different years such as to explain the varying numbers of tetraonids.

22. The conditions after hatching on the other hand display such features, especially in regard to the young chicks' nutritional ecology and physiology, that these circumstances can influence the number of capercaillies in a decisive way.

23. Physiological maturity as well as experience is probably of importance for the development of the feeding activity of the capercaillie chicks.

24. Favourable meteorological conditions especially with regard to the microclimate are necessary to enable the capercaillie chicks to take up sufficient food during their first week of life.

25. During unfavourable weather conditions the chicks starve, and after the main part of the yolk sac has been resorbed their fat reserves also are used up. This reduces the thermal insulation of the body still more, and finally the emaciated chicks perish.

26. The first day of life seems to be the least critical from the point of view of weather, as the chicks' food uptake is then quite insignificant. On the other hand the capercaillie chicks are exposed to the destructive influence of rain and cold also after the first week of life.

27. The condition and resistance to starvation of the newly hatched chicks did not vary demonstrably between the two years when the starvation experiments were carried out, although the years were very different from the point of view of reproduction.

28. Thus the meteorological conditions during the period of reproduction are of fundamental importance to the reproductive capacity of the capercaillie, and ought also to influence in a decisive way the fluctuations of the capercaillie population of our country.

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